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Ivan Murray Johnston

JOURNAL
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IVAN MURRAY JOHNSTON, 1898–1960

RICHARD A. HOWARD

With portrait *

IVAN M. JOHNSTON was born in Los Angeles, California, on February 28, 1898, the son of William Murray and Etta Farnsworth Johnston. He died suddenly on May 31, 1960. His career was devoted to taxonomic botany, and, by combining field work with herbarium study, he was able to bring to his many publications an intimate knowledge of the plants about which he wrote. Few men of his generation did this so well, and fewer students today are developing this ability.

Johnston's interest in local flora and field observations was stirred while he was still a student in high school. He collected plants and sent specimens to the botanical leaders of this period, each with critical observations not usually associated with a student of his age. His college work was begun at Pomona College (1916–1918) before he transferred to the University of California at Berkeley where he received his A.B. degree in 1919. During these formative years he was influenced by T. S. Brandegee, Alice Eastwood, Harvey M. Hall, W. L. Jepson, P. A. Munz, S. B. Parish and W. A. Setchell, each of whom can be associated with some aspect of his future work. Hall and Parish guided Johnston to his work on the San Gabriel Mountains of California, Setchell and Brandegee to the work on Baja California and the desert vegetation of Mexico, and Jepson to the work on the family Boraginaceae which was to become Johnston's most significant contribution. Munz was his collaborator on many papers and Miss Eastwood his ideal of botanical efficiency. Johnston also received his M.A. degree from the University of California (1922) before coming to Harvard in the Fall of that year to continue his work towards his doctorate which he received in 1925.

During his undergraduate years he did field work in the San Gabriel mountains with S. B. Parish and in the vicinity of Claremont, California with P. A. Munz. Some of the troublesome specimens were sent to Macbride at the Gray Herbarium, and thus began a correspondence that led

* This portrait was taken by Ernst Abbe in 1942 at the Gray Herbarium, Cambridge, Massachusetts.

eventually to Johnston's application to Harvard for graduate work and a long association with the Gray Herbarium. In 1918, Johnston expressed his annoyance to Macbride that *Amsinckia* and *Cryptantha* were in a "mess." Macbride subsequently named the specimen which had bothered him *Cryptantha intermedia* var. *johnstonii*. Another collection sent to Rydberg was named by him *Rosa johnstonii*. These two appear to be the first of nearly a dozen taxonomic epithets commemorating Ivan Johnston's active botanical role.

During the summers of 1919, 1920 and 1922 Johnston worked as an assistant at the Alpine Laboratory of the Carnegie Institution near Boulder, Colorado. He served as assistant and companion to Dr. Harvey Hall in ecological studies involving the transplanting of paired species of restricted distribution from one environment to another to determine the effects of soils, altitude and genetic factors on the tolerance, adaptability and the morphological characteristics of the species. This early training created in him an awareness of soil types in relation to plant distribution which was to be present in all his botanical observations in future years and which, in many ways, was influential in his taxonomic decisions.

The summer of 1921 Johnston spent on a California Academy of Sciences expedition to the Gulf of California as the official botanical collector. He wrote to Macbride, "The expedition touched on every island of the Gulf of California and at a number of localities on the Sonoran and peninsular coasts. I had the time of my young life as you may imagine. I got about 1400 numbers which aggregate in the neighborhood of 8000 specimens." Encouraged by Macbride's subsequent interest, Johnston made his plans to go to Cambridge for graduate work. He was awarded an Austin Fellowship but chose instead employment offered by B. L. Robinson as herbarium assistant in the Gray Herbarium. He was listed as such on the Gray Herbarium letterhead for the years of his graduate work. Johnston completed his graduate work in 1925 with a thesis on "The North American Species of *Cryptantha*." He was awarded a Sheldon Travelling Fellowship by Harvard which he used for a long trip to Chile, departing from New York on October 1, 1925, and returning on May 31, 1926. His field work in Chile was both energetic and successful. Physically active and personable he made many friends on the boat trip south and received invitations to visit remote areas for his collecting. His interest in following the desert routes of Philippi, as well as entering into new areas, led him from the driest of desert areas to Andean locations at 17,000 feet. Many of his collecting areas have not been revisited as they represent remote locations difficult to reach. The work on these collections was to occupy him for many years and necessitated trips to European herbaria for study in 1927, 1929 and 1932–1933. The last trip to Europe, made on an award of a Guggenheim Fellowship, served as a wedding trip and established contact with many European botanists.

Following the death of Charles Sargent, director of the Arnold Arboretum, in 1930, Prof. Oakes Ames was appointed supervisor of the botanical collections of Harvard University. Professor Ames secured the resig-

nation of Johnston as senior assistant at the Gray Herbarium and his appointment as research associate at the Arnold Arboretum on August 1, 1931. This appointment was to enable Johnston to continue his field work in South America and his work on the Boraginaceae. Ames had extensive plans for Johnston to return to Chile, to visit the central Andean region, and to extend the interests of the Arboretum to Argentina and Brazil. The program for exploration was delayed but Johnston's intense interest in the flora of the desert areas of South America persisted to the end of his life.

For the remainder of his professional career Johnston was associated with the Arnold Arboretum. To enable him to teach within Harvard College, Johnston was appointed a lecturer in 1934, and in 1938 he was given the title of Associate Professor. After the retirement of Dr. E. D. Merrill as director of the Arnold Arboretum in 1947, Prof. Karl Sax was made acting director and Dr. Johnston supervisor of the herbarium and library. He served as associate director of the Arnold Arboretum from 1948 until 1954.

Johnston's courses, offered as a teacher, were of varying quality. Most outstanding was a survey of the families of flowering plants where his field knowledge of so many families, coupled with his comprehensive knowledge of the botanical literature, made the presentation of great value to the many students who enrolled in or audited the course. He supervised the graduate work of three students, one Chinese, one Indian and one American.

The encouragement of Ames, and later Merrill, for Johnston to return to the field work which he previously had done so productively and so well was not successful until 1938, when he completed the first of three trips (1940, 1941) to the intermontane plateau and the deserts of northern Mexico. These trips were made with the coöperation of the Desert Laboratory of the Carnegie Institution. The most significant results of these trips were his papers on the relationships of floras of North and South American deserts and on the relation of vegetation types to soils, e.g., the gypsophile plants. Johnston started a series of papers on the species composition of the flora of the Coahuila area, and articles dealing with the pteridophytes, gymnosperms, monocotyledons, and the dicotyledons through the family Nyctaginaceae were published. The remainder of the collection was never studied.

During World War II, Johnston was called upon as a civilian for his botanical knowledge. He worked first in Massachusetts on the problems of using plant materials as camouflage and later, in Panama, supplied botanical data for studies of means of defoliating tropical forests by the use of chemicals. His papers on the flora of San José Island and other areas of the Isthmus of Panama present aspects of this service. He was cited by the United States Army for these contributions.

In the post-war years Johnston's botanical interests became more varied. His work with the pollen of *Lithospermum* caused him to consider seriously devoting his time to the field of palynology. An opportunity for contract work with the United States Army in Panama changed his in-

terests again to ecology, and in 1955–1956 he made four trips to Central America collecting data. At the end of his career he had returned to a study of the flora of the southwestern United States and adjacent Mexico through his coöperation with a project on the flora of Texas. A manuscript treatment of the Boraginaceae of Texas was almost complete at the time of his death. This, along with all his personal library and botanical records has been deposited at the Texas Research Foundation, Renner, Texas.

It was during this post-war period that Johnston became involved in a controversy with Harvard University officials and many of his colleagues. He sided with those opposing the move of any portion of the herbarium, library or staff of the Arnold Arboretum to the new herbarium building in Cambridge. The move was completed in 1954, but the controversy was not resolved at the time of his death.

Ivan M. Johnston had been a member of the American Academy of Arts and Sciences, the American Society of Plant Taxonomists, the Botanical Society of America, the New England Botanical Club, Sigma Xi, Gamma Alpha, the International Association of Plant Taxonomists, and a corresponding member of the Chilean Society of Natural History and the Argentine Society of Natural Sciences.

He is survived by his widow, Mildred Williamson Johnston, a son, William, and a daughter, Elizabeth (Mrs. Frederick Milleker).

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* Compiled by Lazella Schwarten.

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Some noteworthy American Borages. [Studies in the Boraginaceae XXX.] Wrightia **2:** 13–22.

THE GENERA OF ERICACEAE IN THE SOUTHEASTERN UNITED STATES [1]

CARROLL E. WOOD, JR.

ERICACEAE Jussieu (HEATH FAMILY)

Trees or shrubs to herbs or fleshy parasites, rarely trailing or scrambling vines [or epiphytes], almost all of acid soils and mostly with mycorrhizal associations. Leaves alternate or sometimes opposite or whorled, simple,

[1] Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University which has been made possible through the support of George R. Cooley and the National Science Foundation. This treatment (which includes Monotropaceae and Pyrolaceae) follows the pattern established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958) and continued through those in volumes **40** and **41**. It should be repeated that the area covered by this work is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area with any supplementary material in brackets. The key (which attempts to avoid switching from flowering to fruiting material) is designed for the species of this area. References which I have not seen are marked by an asterisk.

The preparation of this study of Ericaceae has led into unexpected byways, and the results are somewhat more voluminous than had been anticipated. The group is one which has long attracted attention, and, in addition to the taxonomic difficulties, the literature is formidable. On the other hand, the numerous published studies have begun to provide real bases for an understanding of the complex biological problems, and the many papers have been most gratefully drawn upon. The outlines of the family itself seem clear, but those of the subfamilies and tribes are subject to very different interpretations. At the generic level knotty problems were encountered especially in the Andromedeae, in which *Andromeda* was long used as a catchall; I am satisfied with the generic limits of all of our members of the tribe with the possible exception of *Leucothoë*, in which § *Eubotrys* is still something of a snag. The generic treatment of *Vaccinium* is another thorny question, and on the subgeneric classification of this and *Rhododendron* taxonomic conclusions are anything but unanimous. Difficult problems in variation at the specific level are present especially in *Rhododendron* and *Vaccinium*, both of which I am glad to be able to leave in abeyance.

Many people have contributed generously to this study. In addition to the valued comments of my immediate colleagues and the careful help of Mrs. Gordon W. Dillon in the preparation of the manuscript, I am grateful for their assistance with specimens or information to R. B. Channell, G. R. Cooley, W. H. Duncan, R. J. Eaton, Mrs. J. Norman Henry, J. Kucyniak, Miss Clermont H. Lee, Mrs. E. O. Mellinger, J. D. Ray, L. E. Richardson, H. F. L. Rock, and E. T. Wherry. Henry T. Skinner has kindly read the manuscript on *Rhododendron*, R. A. Howard has generously given me access to his unpublished data on the nodal anatomy of members of the family, and J. L. Thomas has struggled valiantly with some frustrating cytological material. I have also been privileged to check a number of distributions against the mounted materials of the herbarium of the Department of Botany at the University of North Carolina at Chapel Hill. The eight generic illustrations are the continuing and careful work of Dorothy H. Marsh.

exstipulate, often coriaceous and persistent [frequently needle-like]; nodes with one trace from one gap. Flowers bisexual (rarely functionally unisexual and the plants dioecious), characteristically regular, in some irregular (mostly by displacement), most commonly 5(4–7)-merous, typically obdiplostemonous, the insertion hypogynous to epigynous. Inflorescences basically racemose (racemes, panicles or corymbs), the individual flowers in the axils of leaves or bracts, the pedicels typically with 2 lateral bractlets. Perianth usually biseriate (the calyx reduced in *Monotropa*). Calyx 4–7-lobed or sepals distinct, usually persistent, valvate, imbricate or reduplicate in bud. Corolla of 4–7 sometimes distinct but usually united petals, often funnelform, campanulate or urceolate, convolute or imbricated in bud. Stamens usually twice or (less frequently) equal the number of petals, usually inserted at the edge of a nectariferous, variously lobed disc [rarely epipetalous], distinct, the filaments often flattened, dilated, or S-shaped [united in some tropical Vaccinioideae]; anthers becoming inverted in development, dehiscing from the base (the apparent apex) by longitudinal slits, clefts, or pores, often with terminal awns or abaxial spurs; pollen grains in tetrads or single. Gynoecium syncarpous, the carpels [2]3–7[–10], typically 4 or 5; stigma simple, often lobed; style single, with a stylar canal with as many rays as locules and continuous with the locules; ovary 1, superior, half-inferior or inferior, typically with as many locules as carpels, the placentation axile, but sometimes loculate below and 1-locular above, the placentation then axile below, parietal above, or with twice as many locules as carpels by the development of additional partitions; ovules anatropous to campylotropous, 1-integumented, numerous to 1. Fruit a loculicidal or septicidal capsule, berry, or drupe, the calyx usually persistent, rarely accrescent and fleshy. Seeds usually small, sometimes winged or tailed; embryo small (in parasitic forms very much reduced), straight, with fleshy endosperm. Base chromosome numbers 6, 8, 12, 13, 19, 23. (Including Monotropaceae, Pyrolaceae, Vacciniaceae.) TYPE GENUS: *Erica* L.

A family of about 75–80 genera and some 2000 species, widely distributed, mostly in acid soils, from sea level to high elevations in the tropics, and throughout the temperate regions of both hemispheres (although largely lacking in Australia where replaced by Epacridaceae), some extending into the arctic. About 35 genera occur indigenously in the United States, 20 in our area. *Erica* L. and *Calluna* Salisb. are naturalized to the north of our area.

Ericaceae share the syncarpous gynoecium with single stigma, style, and ovary, the style with a fluted canal continuous with each locule; the flowers generally with sympetalous corolla; the androecium typically obdiplostemonous, the usually distinct stamens from the edge of a nectariferous disc; the anthers inverted either in development or at anthesis, opening by morphologically basal pores or slits or longitudinally; and the pollen usually in tetrads (with the exception of Monotropoideae and a few others). Some of the apopetalous genera appear to be primitively so (e.g.,

Befaria, *Elliottia*) but others seem to be derived types (e.g., *Ledum*, *Pyrola*, *Chimaphila*, *Monotropa*). The group is predominantly woody with specialized forms herbaceous (e.g., species of *Gaultheria*, Pyroleae, Monotropoideae).

The family is further characterized by a well-marked combination of embryological features found only in the Ericales: ovules with a single integument and thin, evanescent nucellus, a more or less differentiated endothelium, a lack of parietal cells; embryo sac of the Polygonum type from a single archesporial cell which functions directly as the megaspore mother cell; endosperm cellular, the first two divisions transverse; the formation of endosperm haustoria at both ends of the embryo sac (with a few exceptions); single-layered seed coat formed from the outermost layer of the integument; endosperm fleshy, the embryo straight; anthers lacking a fibrous layer, the tapetum with multinucleate cells; pollen grains 2-celled and (in most instances) adhering in tetrads.

Structurally and embryologically the Ericaceae are clearly related to Clethraceae and Cyrillaceae, on the less specialized side, and to Epacridaceae and Empetraceae, on the more specialized, the five constituting the Ericales.

Subfamilial categories are not well agreed upon, and the limits of the family itself have been variously interpreted, some authors separating Pyrolaceae, Monotropaceae, and Vacciniaceae. However, Pyroleae and Monotropeae appear to be related to Andromedeae and Arbuteae, and, with the exception of the herbaceous or parasitic habit and attendant modifications, the features are all those of Ericaceae (Henderson, Copeland). The Vaccinioideae differ only in the partially to completely inferior ovary (cf. *Gaultheria*) which becomes baccate or drupaceous in fruit (cf. Arbuteae, Monotropoideae); separation as a family on the basis of this one character seems hardly justifiable. The Ericaceae are here treated as composed of subfamilies Ericoideae (including Rhododendroideae, Arbutoideae, Pyroloideae), Monotropoideae, and Vaccinioideae; five tribes (by some regarded as eleven) occur in our area.

The family includes both small, isolated, well-marked genera and large, polymorphic complexes with indistinct generic lines. Within genera species may be similarly distinct or complicated. Polyploidy is frequent in some genera.

The flowers of most are showy, those of the temperate areas being adapted for pollination by insects (or those of some tropical species by birds). The stamens of species with campanulate to urceolate pendent flowers are often appendaged in such a way that the disturbance of the anthers by an insect visitor and the sifting out of pollen are insured. In species with horizontal flowers and exserted stamens, on the other hand, the stamens are unappendaged but the pollen tetrads are often linked by viscin strands so that the entire mass is pulled from the anther as a cobwebby net. In Andromedeae the anthers frequently have disintegration tissue which produces powdery white areas (of apparently unknown function) in the connective.

Economically the group is notable chiefly as a source of showy ornamental woody plants, but various species of *Vaccinium* (blueberries, cranberries, mountain cranberries) are of increasing importance for their fruits.

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ARTIFICIAL KEY TO THE GENERA OF ERICACEAE IN THE SOUTHEASTERN UNITED STATES

(Based upon flowering material, with subsidiary characters from the fruit.)

A. Plants woody or herbaceous, autotrophic, with green leaves; pollen in tetrads.
  B. Petals distinct; ovary superior.
    C. Plants woody, shrubs or small trees; flowers 4–7-merous; ovary 3–7-locular, the placentae axile; capsule septicidal.
      D. Ovary 2-, 3-, or 7-locular; ovules anatropous; seeds not winged; evergreen shrubs.
        E. Ovary 7-locular; petals 7; stamens 12–20 (usually 14); flowers showy, in terminal racemes, producing quantities of sticky nectar. ..... 1. *Befaria.*
        E. Ovary 2- or 3-locular; petals 5; stamens 10; flowers small, in umbel-like inflorescences. ..... 4. *Leiophyllum.*
      D. Ovary 4- or 5-locular on the same plant; ovules flat, sessile on the massive placentae; rarely fruiting; seeds winged all around; deciduous shrub or small tree with racemes or panicles of white flowers with recurved petals. ..... 2. *Elliottia.*
    C. Plants herbaceous, evergreen, with slender subterranean rhizomes; flowers 5-merous; ovary 5-locular below, 1-locular above, the placentae axile below, becoming parietal above; capsule loculicidal.
      F. Inflorescence corymbose; flowers regular; filaments hairy, enlarged at or below the middle; style short, straight; capsule valves with smooth margins. ..... 15. *Chimaphila.*

F. Inflorescence racemose; flowers more or less irregular; filaments glabrous, not enlarged in the middle; style declined; capsule valves with cobwebby margins. ..... 16. *Pyrola*.

B. Petals united (usually conspicuously so) or, if appearing distinct, the ovary inferior (some species of *Vaccinium*).

G. Stamens with disintegration tissue (appearing white, powdery) on the apparent abaxial side at the top of the filament or in the connective or upward on the anther-halves, the anthers or filaments often appendaged (or if stamens aborted or not opening see 14. *Epigaea*); fruit a loculicidal capsule (the calyx fleshy in *Gaultheria*, surrounding the fruit and appearing berry-like).

H. Plants low, subherbaceous, evergreen, with underground rhizomes; anther-halves with 2 terminal awns; flowers solitary in the axils of leaves, with a pair of bracteoles immediately beneath the calyx; calyx accrescent, fleshy, berry-like; seeds with hard coats. ..... 8. *Gaultheria*.

H. Plants erect, conspicuously woody, shrubs or trees; calyx not accrescent; seeds with thin, loose coats.

I. Inflorescence clearly elongate, racemose or paniculate; capsule margins not differentiated.

J. Anthers appendaged on the abaxial side with 2 stout, reflexed spurs just above junction with filament, these lacking white disintegration tissue; each anther-half with a line of disintegration tissue extending upward above spurs; corolla glabrous; evergreen shrubs with terminal and axillary racemes. ..... 11. *Pieris*.

J. Anthers not appendaged on abaxial side, with or without terminal awns.

K. Corolla puberulous without; deciduous trees with terminal panicles; stamens unappendaged, with a small area of disintegration tissue near apex of each anther-half; capsule ovoid-pyramidal. ..... 13. *Oxydendrum*.

K. Corolla glabrous; deciduous to evergreen shrubs with terminal and axillary racemes; anthers with or without 2 or 4 terminal awns, with white disintegration tissue in angle between awns or this position when lacking awns; capsule depressed-globose. 7. *Leucothoë*.

I. Inflorescences of corymbose clusters (reduced racemes) in axils of leaves or bracts (sometimes thus a raceme of corymbs) of the same or preceding season.

L. Stamens with 4 prominent terminal awns; disintegration tissue in a conspicuous patch below awns; shrub with white, broadly campanulate flowers on wood of preceding season. ..... 9. *Zenobia*.

L. Stamens without terminal awns, with or without reflexed spurlike appendages on upper part of filament (these, when present, with a margin of white disintegration tissue extending upward onto the anther-halves); carpel midrib differentiated (colored or thickened), and to varying degrees splitting away separately from valves in fruit; evergreen

to deciduous shrubs with globose-urceolate to cylindric corollas. ..... 10. *Lyonia.*

G. Stamens lacking white disintegration tissue on apparent abaxial side. (If not opening or aborted, see 14. *Epigaea.*)

M. Ovary superior; stamens unappendaged; fruit a capsule.

N. Corolla saucer-shaped, with 10 pouches in which the anthers are held in bud. ..... 3. *Kalmia.*

N. Corolla various, without pouches for the anthers.

O. Flowers 4-merous; corolla campanulate or urceolate; stamens included; anthers opening by short slits; capsule septicidal. ..... 5. *Menziesia.*

O. Flowers 5-merous.

P. Stamens conspicuously exserted; anthers not tapering, opening by terminal pores; flowers showy, in corymbose inflorescences from buds of the preceding season; capsule septicidal. ..... 6. *Rhododendron.*

P. Stamens included; capsule loculicidal.

Q. Anthers tapering into tubular beaks, opening by terminal pores; flowers bisexual; corolla oblong-urceolate; flowers solitary in the axils of reduced foliage leaves; scurfy-leaved shrub of bogs. ..... 12. *Cassandra.*

Q. Anthers opening along the entire length; plants functionally dioecious, the stamens aborted or not opening in carpellate flowers; corolla salverform; flowers in the axils of bracts; trailing broad-leaved evergreen subshrub. ..... 14. *Epigaea.*

M. Ovary inferior or half-inferior; fruit fleshy.

R. Ovary half-inferior; flowers 4-merous; each anther-half with a bifurcate terminal awn; diminutive creeping subherbaceous plant of cold mountain bogs, the solitary flowers in the leaf axils; fruit white. ..... 8. *Gaultheria.*

R. Ovary inferior; flowers 4- or 5-merous; anthers without terminal awns but the anther-halves more or less prolonged and tubular; inflorescences various; fruit black, blue, or red (very rarely white).

S. Ovary 4- or 5-locular, or 10-locular above by the development of partial false partitions; ovules numerous; fruit a many-seeded, fleshy to leathery berry; anthers with or without spurs on the abaxial side. ..... 19. *Vaccinium.*

S. Ovary 10-locular, 10-ovuled, becoming baccate-drupaceous with 10 hard nutlets; anthers unappendaged. ..... 20. *Gaylussacia.*

A. Plants herbaceous, parasitic, lacking chlorophyll, with reduced scalelike leaves, variously colored; pollen grains single.

T. Petals united; calyx of 5 regular sepals; fruit a berry. ..... 17. *Monotropsis.*

T. Petals distinct, saccate at the base; calyx represented by 1–5 scale- or bractlike sepals; fruit a loculicidal capsule. ..... 18. *Monotropa.*

Subfam. ERICOIDEAE Endlicher ('Ericinae')

Tribe RHODOREAE D. Don [2]

1. **Befaria** Mutis ex Linnaeus, Mantissa Pl. 152, 242. 1771.

Evergreen shrubs [or small trees, rarely to 20 m., but with slender trunks] with alternate, more or less coriaceous, persistent, usually entire, obovate to elliptic [or rarely linear], flat [or revolute-margined], short-petioled leaves. Flowers showy, 7(5–8)-merous, in terminal (and sometimes axillary) racemes [or, by reduction, corymbs]. Calyx campanulate, 7-parted, the lobes persistent. Petals usually 7, free, narrow, linear- to obovate-spatulate, white or pinkish [to red], imbricate in aestivation (the odd petal abaxial). Stamens hypogynous, 12–20 (usually 14), the filaments free, elongate, dilated at the base, pubescent below; anthers dorsifixed, muticous, dehiscing by 2 oblique slits at the apex, without dis-

[2] According to changes adopted by the IX International Botanical Congress (1959) modifying Article 19 of the International Code of Botanical Nomenclature (to read, in part, "The name of any taxon of a rank below family and above genus which includes the type of the next higher taxon must be based on the same stem as the name of the next higher taxon, but, contrary to Article 46, without citation of an author's name"), the correct name for this tribe is "Rhododendreae" if subfamily Rhododendroideae Endl. is recognized as distinct from Ericoideae. Fortunately, in the Ericaceae only this tribe is likely to have two possible correct names, depending upon the subfamilial classification adopted, for most of the proposed subfamilies (all of later date than the tribes) reflect the name of an included tribe. However, other well-known tribal names (Ericeae, Monotropeae, Pyroleae, Vaccinieae) of David Don, who first blocked out these basic units of the family in 1834, may have to be cited without an author. Other families may not fare so well. Under the principle of the repetition of generic or subgeneric names for included subgenera and sections, already in use in Article 22 of the Code and now to be embodied in Articles 17 and 19, precisely the same taxon in large and complex orders, families, or genera may have alternative names (and types) depending upon the taxonomic ideas of the author as to the next higher category.

In connection with the effects of Article 22, G. L. Webster has aptly commented (Jour. Arnold Arb. **41**: 279. 1960), "This ruling is unfortunate, in my opinion, since it fallaciously assumes a parallel between typification of a genus or species with that of a subgenus. The subgenus does not appear in the name of the species and is a purely intercalary category, as is the section. That the new rule does not really contribute to stability is shown in the present case. If subgenera are recognized in *Phyllanthus*, the epithet of this section must be *Kirganelia*; but if one chooses not to recognize subgenera then the same section must take the epithet *Anisonema*." While it may be useful to have the type family of an order reflected in the subordinal categories, the type genus of a family in the subfamilial categories, the type species of a genus in the subgeneric categories, the extension of this principle to every subordinate taxon between the rank of order and series would seem to lead only to confusion and obfuscation of formerly clear taxa and to work against the interests of nomenclatural stability and taxonomy. This principle seems to the writer to have been considerably overextended. Since, pending formal publication of a new edition of the Code, these changes are not yet binding, the 1956 edition is followed here and authors are cited for subfamilial and tribal names. (For a further example of name switching engendered by Article 22 see the subgeneric categories in *Rhododendron*, and, for an exercise in total confusion, attempt to correlate nomenclaturally and taxonomically the classifications adopted by Rehder, Sleumer, Seithe-von Hoff, and the present author!)

integration tissue; pollen tetrads with viscin strands. Stigma depressed-capitate, 7-grooved; style terete, elongate, bent to one side; ovary superior (or the base slightly immersed in the receptacle), 7-sulcate, 7-locular, with numerous elongate ovules on large axile placentae. Capsule erect, depressed globose, surrounded at the base by the persistent calyx and terminated by the elongate style, 7-valved, septicidal from the apex. Seeds numerous, elongate, narrow, curved, tapered, some angled by compression. (*Bejaria* Vent.) TYPE SPECIES: *B. aestuans* L. (Described from Mutis' manuscript, the name, apparently intended in honor of Mutis' friend José Bejar, professor of botany at Cadiz, misread and written consistently by Linnaeus as *Befaria*, rather than *Bejaria*.)

Perhaps 10–30 species in two sections: *Befaria racemosa* Vent. in our area; *B. cubensis* Griseb. in western Cuba; four or more species in Mexico, Guatemala, and Honduras; the remainder in the Andes, from Venezuela to Bolivia, and on the disjunct table-topped mountains eastward to Mt. Roraima. Mansfeld and Sleumer recognized 20 species in South America, whereas Camp has suggested that as few as four basic species may account for the range of variation, the difficulties in delimiting taxa being ascribed to hybridization.

Befaria racemosa, a shrub 1–2.5 m. tall, with sparsely hispid twigs and conspicuous, fragrant, white flowers in winter, spring, or early summer, occurs in flatwoods and sand-scrubs from Dade, Highlands, and Lee counties, Florida, northward to Camden, Glynn, and Worth counties, Georgia. Nectar is produced copiously from the glandular inner surface of the calyx, hence the name tar-flower or fly-catcher. The species lacks a hypodermis in the leaves, in contrast to all other species, and differs further in the elongate raceme (or panicle) much exceeding the leaves. It is relatively invariable and isolated within the genus and is the sole member of sect. RACEMOSAE Fedtsch. & Basilev. According to Mansfeld and Sleumer its closest relatives are *B. glauca* Humb. & Bonpl., of Colombia, and *B. laevis* Benth., of Mexico, the two later united under the former name by Camp. *Befaria cubensis*, geographically nearest to *B. racemosa*, is a very different and highly specialized plant, presumably most closely related to *B. ledifolia* Humb. & Bonpl., of Colombia.

Copeland has shown that *Befaria* shares with *Elliottia* and *Cladothamnus* viscin strands among the pollen tetrads and resorption tissue in the anthers, a combination found nowhere else, but differs from them in having haustoria at both ends of the endosperm and in the opening of the anthers by a brief slit. It is unique among genera of Rhodoreae in the trilacunar vascular supply to the sepals and in the opening of the anthers by the formation of a cleft between intact cells (rather than by collapse or resorption of cells). On the basis of these features, as well as the gross morphology of the flower, the genus was set apart by Copeland as a tribe and regarded as the most primitive of the Ericaceae. In wood structure, however, "*Befaria* [5 species of sect. BEFARIA] is more advanced than several of the lower genera of other tribes" (Cox). In a comparison of

Befaria with *Clethra* Copeland concluded, "The effect of this comparison is to show that while *Clethra* and the Rhododendroideae are descended from a common ancestor, this ancestor and all transitions between it and the groups named have disappeared, leaving the survivors quite isolated."

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2. **Elliottia** Muhlenberg ex Elliott, Sketch Bot. S. C. & Ga. 1: 448. 1817.

Deciduous tree to 6 (9) m., or often a shrub to 3 m., with gray bark, the twigs chestnut-brown. Leaves alternate, petiolate, oblong or oblong-elliptic, the apex acute, the base cuneate, membranaceous, pale and pubescent beneath. Inflorescences terminating the growth of the season, elongate panicles or loose racemes 8–25 cm. long, the flowers slightly irregular, slender-pediceled, with deciduous, subulate bracts. Calyx small, 4(5)-lobed, persistent. Petals 4 (or almost as frequently 5 in the same inflorescence), free, oblong-lanceolate, recurving, white. Stamens 8 (10), the filaments flattened, the anthers 2-lobed at the base, the apex apiculate, opening almost from base to apex by 2 V-shaped areas of resorption tissue; pollen tetrads with viscin strands. Stigma discoid-capitate, with 4 (5) grooves; style longer than the petals, thickened and incurved above, soon deciduous; ovary superior, 4(5)-locular, on a 4(5)-lobed disc (gynophore?); placentae large, the ovules 5–8 in each locule, strongly flattened, sessile. Fruit a depressed-globose 4(5)-lobed capsule (8–12 mm. broad), sometimes with a very short gynophore, septicidally dehiscent from above, the valves and enlarged placentae persistent; seeds 1–several in each locule (many ovules aborting), discoid, winged all around, strongly compressed between placenta and ovary wall, 3–4 mm. across, falling from the placenta. TYPE SPECIES: *E. racemosa* Muhl. ex Ell. (Named for Stephen Elliott, 1771–1830, distinguished South Carolina botanist.)

One to three very distinct species, depending upon the generic concept; *Elliottia racemosa* in our area, two others in Japan (see below).

Elliottia racemosa, with numerous showy panicles or racemes of 40–80 white flowers produced in June or early July, is one of the handsomest,

as well as one of the rarest, of our native shrubs. It apparently is largely confined to isolated colonies in mediacid sandy soils (Norfolk sand) of the Coastal Plain in an area roughly bounded by Aiken County, South Carolina (where it is now presumed extinct), and Columbia, Screven, and Coffee counties, Georgia. Although usually seen as a shrub where subjected to burning, in its best development the plant is a small tree to 9 m. tall and grows in moist but always well-drained sands in mixed woods within a few hundred feet of streams. The plant shows a considerable range of tolerance, however, and some colonies are in rather dry locations, on oak ridges, in *Pinus australis* savannas, or in *Pinus-Quercus* woods. (In cultivation, given an acid and well-drained soil and an eastern or southern slope, it is hardy at least as far north as Philadelphia.)

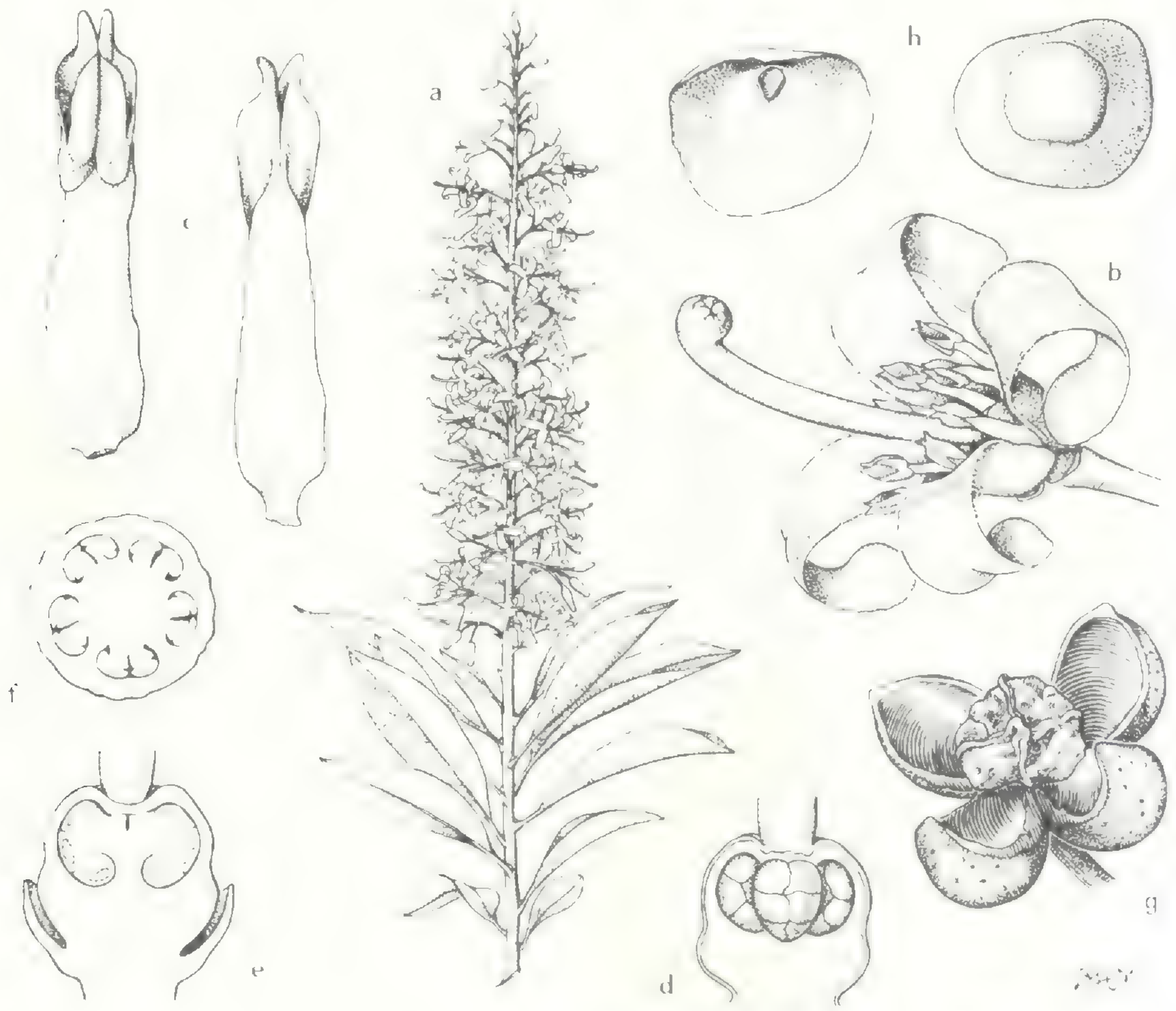

FIG. 1. **Elliottia.** a–h, *E. racemosa*: a, flowering branch, ca. × 3/8; b, flower, × 3; c, stamens, inner and outer views, × 10; d, four-locular ovary, half of wall removed to show sessile ovules on placentae in three locules, × 10; e, ovary and calyx in vertical section, showing sessile ovules on massive placentae, semi-diagrammatic, × 10; f, five-locular ovary in cross section, showing divided placentae, sessile ovules, × 10; g, open 4-carpellate capsule after shedding of seeds, × 4; h, inner and outer views of thin-winged seed, × 4.

At a number of the known stations *Elliottia* apparently seldom or never fruits, and a number of misconceptions concerning fruits and seeds have remained in the literature. (See Drude, Copeland; but see Wherry for an accurate description.) In at least two localities fruits are produced, how-

ever, and reproduction by seedlings has been found. (It is perhaps significant that these stations are relatively moist.) The lack of fruiting has led to the supposition that each colony is clonal and self-sterile, but no evidence of root-suckering or clonal connections between plants has been produced. (The plant suckers abundantly from the stem-base after burning or cutting, however.) Chromosome counts, further observations on the pollination mechanism, and artificial crossing experiments are suggestive lines of approach to the problem. Copeland observed in preserved material that the pollen is shed in the pendent bud, falling in four cylindrical masses from each anther and lodging in the apex of the closed corolla beyond the stigma. He supposed that as the style elongates the pollen is pressed against the spoonlike tips of the petals by the stigma, and then exposed as the flower rises to the horizontal and the petals recurve.[3]

Lack of unanimity has characterized the generic treatment of *Elliottia racemosa* and the two Japanese species, both of which have five sepals, three petals, six stamens, and a three-locular ovary. *Tripetaleia paniculata* Sieb. & Zucc. (*E. paniculata* (Sieb. & Zucc.) Benth. & Hook.), a shrub of Kyushu, Shikoku, Honshu, and Yezo, resembles *E. racemosa* in many respects, but for the smaller, more complex panicles of smaller flowers, the trimerous symmetry, the development of a definite gynophore, and the lack of a well-developed marginal wing on the seed; it may well be included in *Elliottia*. *Tripetaleia bracteata* Maxim. (*E. bracteata* (Maxim.) Benth. & Hook.), a smaller shrub of Honshu and Yezo, is considerably more modified, with comparatively large bracts, reduced, purely racemose inflorescences, subfoliose sepals, an obscure gynophore, and different seeds. Stapf regarded *E. racemosa* and *T. paniculata* as congeneric, but treated the third as *Botryostege bracteata* (Maxim.) Stapf, thinking it closer to *Cladothamnus pyroliflorus* Bong. (distributed from Oregon to Alaska)

[3] A number of the ecological data above were corroborated or supplied by Miss Clermont H. Lee, of Savannah, Georgia, who has also very kindly made additional field observations on the flowers and their opening. She has observed that the buds are upright at first, becoming pendent when about 4–4.5 mm. long. At 5–7 mm. the pollen has started to fall from the stamens onto the underside of the stigma. Eventually it works its way under and around the stigma, there being a space between it and the spoonlike petal tips. At the time of opening of the flower, most of the pollen seems to be adherent to the stigma. Although the contents of most fall out, some anthers continue to contain pollen until anthesis. At anthesis the bud (then about 14 mm. long) has assumed a horizontal position. Some pollen may fall from the spoonlike tips of the petals and some from the stigma as the petals reflex. (Open flowers showed no evident pollen on the petals.) The stigma seemed to be moist at the time the petals began to reflex. "Small yellow bees" were observed climbing and flying over opened and unopened flowers, apparently collecting nectar from the slightly fragrant flowers, their wing tips seeming most often to touch the stigmas. Bees were observed flying from one plant to another. A single hummingbird was also seen to visit the flowers. It was also observed that on the lateral branches of the panicle the terminal (or central) flower of the two or three present opens first, and that sometimes the terminal flower of the panicle was open before those just below. An attempt by Dr. Joab Thomas to secure meiotic chromosomal counts from material from this colony kindly fixed by Miss Lee was unsuccessful, for, although the buds were of the proper size, the pollen mother cells, for reasons unknown, showed a complete lack of divisions.

than to *Elliottia*. Copeland and Cox arrived at opposing conclusions regarding *Elliottia* and *Tripetaleia*, but neither was able to study material of *Botryostege*. Whatever the taxonomic treatment followed, all four taxa are clear-cut, relict species of great morphological and phytogeographic interest.

Copeland characterized his tribe Cladothamneae (which included only these plants) by the free petals, by the anthers opening throughout their length by resorption tissue, by viscin strands among the pollen tetrads, by endosperm without chalazal haustoria, and by the characteristic manner of discharging the pollen. *Ledum* L., associated with these genera by Drude, was removed to a position near *Rhododendron*.

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3. **Kalmia** Linnaeus, Sp. Pl. 1: 391. 1753; Gen. Pl. ed. 5. 185. 1754.

Evergreen or rarely deciduous shrubs or small trees to 12 m. Winter buds with about 2 outer scales. Leaves alternate, opposite or whorled, entire, usually coriaceous, petioled or rarely sessile, glabrous, pubescent, hirsute or glandular. Flowers in terminal or axillary corymbs or solitary in the axils of leaves and forming a loose terminal "raceme"; each flower in the axil of a leaf or (in those species with corymbs) of a small, thick bract, and with a pair of bractlets at the base of the slender pedicel. Flowers 5-merous; base of receptacle impressed. Calyx synsepalous, deeply 5-parted, persistent, or deciduous in fruit. Corolla sympetalous, saucer-shaped, with a short, narrow tube, shallowly 5-lobed, and with 10 pockets

in which the anthers are held. Stamens 10, the filaments slender, the anthers short, unappendaged, opening by apical slits, without white disintegration tissue; anthers lodged in the pockets of the corolla in the bud so that the filaments are strongly recurved and held under tension by the expansion of the corolla and spring up suddenly when the corolla is touched; pollen tetrads with or without viscin strands. Style slender, straight; stigma flat, unexpanded, 5-grooved; ovary superior, 5-locular, with massive placentae and numerous ovules, on a conspicuous disc. Capsule subglobose to globose-ovoid, septicidal, 5-valved, opening from above, the style persistent on the central axis. Seeds numerous, minute, essentially cylindrical, with a loose coat. (Including *Kalmiella* Small.) LECTOTYPE SPECIES: *K. latifolia* L.; see N. L. Britton, N. Am. Trees 756. 1908. (Dedicated to Pehr Kalm, 1716–1779, student and friend of Linnaeus, who travelled and collected in North America from 1748 to 1751.)

About six species of North America, including *K. polifolia* Wangenh. (consisting of vars. *polifolia* and *microphylla* (Hook.) Rehd.), of cold bogs and alpine meadows from Labrador to Alaska, south to Pennsylvania, Minnesota, Colorado, Montana, and California; *K. ericoides* C. Wright ex Griseb. (including *K. aggregata* (Small) H. F. Copel. and *Kalmiella simulata* Britt. & Wilson, based on variations in pubescence and compactness of inflorescence), of Pinar del Río and the Isle of Pines, Cuba; four species in our area.

Kalmia latifolia, mountain laurel, widely distributed in acid soils, largely in deciduous woodland, from western Florida to Louisiana, northward to New England, New York, Ohio, and Indiana, is a shrub, or occasionally a tree to 10–12 m. tall, with elliptic or elliptic-lanceolate, mostly alternate leaves 5–10 cm. long and showy terminal corymbs of white to pink flowers 1.5–3 cm. across, the petioles glandular-pubescent. The plant is a popular horticultural subject and a number of variant forms have been named. (See Rehder, Holmes.) Plants with the pedicels less markedly glandular have been named var. *laevipes* Fern. *Kalmia angustifolia* L. var. *carolina* (Small) Fern. (*K. carolina* Small), a shrub to about 1 m. tall, with short-petioled oblong to lanceolate mostly opposite or ternate leaves, pubescent beneath even at maturity, axillary to terminal corymbs of deep pink or purple flowers about 1 cm. across, ranges from southeastern Virginia southward through eastern North Carolina to eastern South Carolina, and occurs in scattered localities in western Virginia (Carroll County), eastern Tennessee (Johnson County), western North Carolina, and northeastern Georgia (Rabun County). In southeastern Virginia it intergrades with the northern var. *angustifolia* (southeastern Virginia northward through eastern Pennsylvania and New Jersey to Labrador and Hudson Bay and west to northern Michigan) which differs in having the leaves glabrous beneath at maturity. *Kalmia cuneata* Michx. is a distinctive deciduous shrub with oblong-obovate, cuneate leaves, glandular beneath, and almost umbellate corymbs of white flowers about 1.5 across produced from the axils of leaves of the preceding year. One

of the rarest of American shrubs, it is known from wet thickets or shrub bogs in only a few localities in southeastern North Carolina and from an early collection of Nuttall between Camden [Kershaw County], South Carolina, and Statesville [Iredell County], North Carolina.

Kalmia hirsuta Walt. (*Kalmiella hirsuta* (Walt.) Small), a straggly shrub with thin, hirsute, alternate, persistent leaves, of the Coastal Plain from southeastern North Carolina (?) and South Carolina southward to Flagler, Putnam, and Alachua counties, Florida, and west to southernmost Alabama; and *K. ericoides*, a low, revolute-leaved shrub of Cuba, differ from other species in the deciduous calyx (cf. *Lyonia*) and in having the flowers borne singly in the axils of ordinary-sized or somewhat reduced foliage leaves (instead of bracts). The plants are otherwise entirely consistent with *Kalmia* both morphologically and anatomically and there seems to be no real justification for the removal of these species (as *Kalmiella* Small) from *Kalmia*. The six species of *Kalmia* are quite distinct morphological entities which are separated ecologically and/or geographically and perhaps genetically. Artificial hybrids do not seem to have been attempted, and no natural hybrids are known. The chromosomal data reported by Hagerup ($2n = 24$ rather large chromosomes in *K. latifolia* and $2n = 48$ chromosomes about half as large in *K. polifolia*) suggest an interesting pattern of polyploidy which should be investigated further.

The most distinctive generic feature of *Kalmia* is the pollination device. In the flower bud the ten anthers are pushed upward by the growth of the filaments into corresponding pockets in the corolla. As the corolla opens and expands the anthers are held by the pockets and the filaments are bent backward under tension. The weight of a suitably heavy insect displaces the corolla, and frees one or more of the anthers; the filaments snap suddenly upward, showering the visitor with pollen. In *K. latifolia* viscin strands occur in the pollen, which is hurled like a sticky net, while in *K. angustifolia* var. *angustifolia* (and probably *K. polifolia*) the pollen is powdery and dusts the visitor.

The leaves of at least *Kalmia latifolia* and *K. angustifolia* are poisonous to many mammals when eaten. The toxic principle is thought to be andromedo-toxin which is presumably the same as that in other poisonous Ericaceae (including evergreen *Rhododendron* species, *Ledum*, *Leucothoë*, *Lyonia*, and *Andromeda*). A mycorrhizal association, without which growth does not occur, has been demonstrated in *K. latifolia*.

Kalmia, *Leiophyllum*, and seven other small, definitely distinct and rather isolated genera are sometimes segregated as the tribe Phyllodoceae Drude. All are evergreen plants, mostly with ericoid or buxoid leaves; in those with pentamerous flowers the median petal is abaxial; and the seeds generally lack appendages (except in *Kalmia*). As defined by Copeland the tribe is characterized primarily by the presence of resorption tissue involving the epidermis of the anther and by the absence of filaments among the pollen tetrads. The latter characteristic does not hold, however, for viscin filaments have been reported in *Phyllodoce*, *Loiseleuria*, and *Kalmia*. The closest relative of *Kalmia* both morphologically and anatomi-

cally appears to be *Rodothamnus* Reichenb. (including *Kalmiopsis* Rehd.), comprised of two species, *R. Chamaecistus* Reichenb., of the eastern Alps, and *R. Leachianus* (Henderson) H. F. Copel., of the Siskyou Mountains, Oregon. *Rhodothamnus*, *Kalmia*, and *Phyllodoce* Salisb. are regarded as relatively primitive within the group.

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4. **Leiophyllum** (Persoon) Hedwig filius, Gen. Pl. 313. 1806.

Evergreen shrubs, prostrate to erect and to about 1 m. tall with crowded, small (to 1.5 cm. long), leathery, alternate to opposite, oblong to orbicular leaves, the petioles short, articulated at the base. Inflorescences ter-

minal umbel-like simple or compound corymbs, the flowers borne singly in the axils of reduced leaves, each with 2 small lateral bracts at the base of the slender pedicel. Flowers 5-merous; base of receptacle impressed. Calyx lobes 5, free nearly to the base, persistent. Corolla of 5 spreading, equal, white or pinkish petals. Stamens 10, conspicuously exserted, equaling or exceeding the petals; filaments filiform, glabrous; anthers small, almost globular, opening by 2 lengthwise slits, unappendaged, blue to purple or pink, without disintegration tissue; pollen tetrads without viscin strands. Stigma not expanded; style filiform, about as long as the stamens, straight, tapering into the more or less glandular 3- or 2(rarely 4 or 5)-locular, superior ovary which is seated on a conspicuous disc; ovules numerous, axile. Capsule ovoid, 3- or 2(rarely 4 or 5)-valved from the apex, the central axis persistent, pointed, the valves nearly smooth to sharp-tuberculate on the back, the style adhering to one valve or broken away. Seeds numerous, brown, minute, plump, unappendaged, the seed coat reticulate. (*Ledum* † *Leiophyllum* Pers. Syn. Pl. 1: 477. 1805; *Dendrium* Desv. Jour. Bot. Desvaux II. 1: 36. 1813; *Ammyrsine* Pursh; *Fischeria* Sw.) TYPE SPECIES: *Ledum thymifolium* Lam. = *Leiophyllum buxifolium* (Berg.) Ell. (Name from Greek, *leios*, smooth, and *phyllon*, leaf, in allusion to the shining, leathery leaves.) — SAND-MYRTLE.

A single variable species (sometimes treated as two or three) of open habitats on acid rocks and sands from the higher summits of the Smoky and Blue Ridge mountains of North Carolina, Tennessee, and northernmost Georgia, via several disjunct stations to the coastal plain of southeastern North Carolina and northeastern South Carolina, and of the pine barrens of southern New Jersey.

Most of the characters used by Small (habit, petal shape, disc, style/ovary proportions, capsule valves) in distinguishing three species in the genus do not hold, and even those of glandular pubescence, leaf shape and leaf arrangement adopted by Camp in delimiting two species (one composed of two varieties) are not altogether constant. The course of Rehder, who recognized a single species, *L. buxifolium*, composed of three varieties, seems to be most in line with the information presently available. Varietas *Hugeri* (Small) Schneid. (*L. Hugeri* (Small) K. Schum.), considered by Camp to be the basic entity, is a decumbent to erect shrub to about 1 m. tall, primarily of the Coastal Plain of southern New Jersey and the Carolinas (but with a few disjunct stations inland in the latter states and eastern Kentucky) with glandular hairs on the pedicels and with mostly alternate leaves which tend to be oblong and slightly apiculate. Varietas *prostratum* (Loud.) Gray (*L. Lyonii* (Sweet) Sweet [nomen subnudum] sensu Small, Camp, *et al.*), prostrate to almost 1 m. high depending upon the habitat, and with glandular pedicels but mostly opposite, elongate-oval to orbicular leaves which are rarely apiculate, is confined principally to exposed ledges and summits in the higher mountains of North Carolina, Tennessee, and northernmost Georgia. Varietas *buxifolium*, primarily of southern New Jersey, has the leaves and leaf arrangement of

var. *Hugeri* but has glabrous pedicels. It should be noted that vars. *buxifolium* and *Hugeri* may occur together in New Jersey; that at least some plants with glabrous pedicels occur in the Carolinas with var. *Hugeri*; that one New Jersey collection with glandular pedicels has predominantly opposite leaves; that all of the mountain plants have glandular pedicels but that in herbarium materials leaf arrangement is somewhat variable and there are possible evidences of ecological influences; and that leaf shape is far from a dependable characteristic in this genus.

As Camp has noted, the type of var. *Hugeri*, from Table Mountain, Pickens County, S. C., is, unfortunately, biologically closer to var. *prostratum* than to the glandular-pediceled plant of the Coastal Plain; the name is retained tentatively, however, in the sense of Camp, until further information on variation and geography is obtained. Ecological and population studies are very much in order. Of particular interest in an understanding of the genus is the relationship of alternate *vs.* opposite leaves to genetic and ecological factors. Transplant experiments and observations on sprouting after fire and the effect of rapidity of growth on leaf arrangement should provide pertinent information.

Little seems to have been recorded of the biological features of the genus, except that the numerous small flowers (April to June) are very attractive to insects.

Leiophyllum has been associated with *Ledum* in the past, largely on account of the distinct petals, but the relationships of the latter appear to be instead with *Rhododendron*. In wood anatomy *Leiophyllum* lies between *Ledothamnus* Meissn. and *Loiseleuria* Desv.

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5. **Menziesia** J. E. Smith, Pl. Icon. Ined. **3**: *pl. 56*. 1791.

Deciduous shrubs (to about 2 m.) with the general aspect of *Rhododendron* § *Anthodendron*. Branches erect or spreading, the leaves alternate, crowded at the ends, the blades thin, broadly elliptic to obovate, apiculate, often strigose, ciliate, entire, gland-tipped, short-petioled. Winter buds swollen, with several outer scales. Flowers 4[5]-merous, appearing with the leaves, in sub-umbellate (to short-racemose) clusters terminating the branches of the previous year, nodding, the pedicels slender, be-

coming erect in fruit. Calyx small, flat or saucer-shaped, circular or shallowly 4[5]-lobed, glandular-ciliate, persistent. Corolla yellowish white at the base, rose at the tip [or greenish to purplish], campanulate or urceolate [or cylindric and sometimes irregular], the tube stout, [often] swollen, the lobes 4[5], rounded and much shorter than the tube, often erect. Stamens 8 [or 5 or 10], included [or exserted]; filaments subulate, flattened; anthers narrow, linear to linear-sagittate, unappendaged, without disintegration tissue, opening (through collapse tissue) by short slits broadened above; pollen tetrads with viscin strands. Stigma truncate; style columnar, included; ovary 4[5]-locular, superior, obscurely lobed, glandular-hairy [glabrous or pubescent], commonly ovoid; ovules many, axile, elongate; disc 8[10]-lobed. Capsule ovoid, oval or obovoid, firm, rather thick-walled, septicidally 4-valved; the style broken or persistent on the central axis; seeds numerous, linear, abruptly pointed or tailed. TYPE SPECIES: *M. ferruginea* J. E. Sm. (Named in honor of Archibald Menzies, 1754–1842, who served as surgeon-botanist on Vancouver's great expedition of survey, 1790–1795, in the course of which he collected the type species.)

A small genus of disjunct distribution including about five or six species: three or four in Japan and Sakhalin (*Menziesia ciliicalyx* (Miq.) Maxim. vars. *ciliicalyx* and *multiflora* (Maxim.) Makino, *M. purpurea* Maxim., and *M. pentandra* Maxim.); *M. ferruginea* vars. *ferruginea* and *glabella* (Gray) Peck in western North America (Alaska to northern California, Alberta, Idaho, and Wyoming); and *M. pilosa* (Michx.) Juss. in the eastern United States, in rocky upland deciduous woods from Pennsylvania southward to West Virginia, Virginia, North Carolina, northern Georgia, and eastern Tennessee.

Menziesia pilosa is easily recognized by the azalea-like aspect, the terminal clusters of nodding, tetramerous, campanulate, yellowish-white to orange-pink flowers about 6–7 mm. long, and the glandular or glandular-setose, septicidal, ovoid capsule 3–4 mm. long. It is closely related to the western American species, from which it differs primarily in details of pubescence of bud scales, leaves, pedicels, calyx, filaments, and ovary and in shape and size of fruit. Both eastern and western species are far from stable in most of these features and the full range of variation has not been adequately described in either group (e.g., the undersurfaces of the leaves of *M. pilosa* vary from densely pilose with short, nonglandular hairs in much of its range to almost glabrous with scattered glandular hairs along the veins in some high-mountain localities in North Carolina).

The American species are characterized by reduced calyces, regular corollas, and tetramerous symmetry, while the Japanese have more prominent calyces, more or less irregular corollas (some almost cylindric and about 1.5 cm. long), and prevailingly pentamerous symmetry (although with a tendency toward tetramery and reduction in the number of stamens). The genus presumably stands nearest *Rhododendron* from which it differs most obviously in the included stamens and the opening of the

anthers by short slits, rather than by pores. In *Tsusiophyllum* Maxim. (monotypic, Japan), in which the stamens are ten, the corolla 5-lobed, and the ovary 3-locular, the anthers open by longer slits, so that in this respect *Menziesia* stands between *Tsusiophyllum* and *Rhododendron*. In wood anatomy, however, *Tsusiophyllum* is more highly specialized than either and is on a level with *Ledum* L. which was placed near *Rhododendron* by Copeland.

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6. **Rhododendron** Linnaeus, Sp. Pl. 1: 392. 1753; Gen. Pl. ed. 5. 1754, *"Rhododendrum."*

Evergreen or deciduous shrubs (rarely trees) [sometimes epiphytes], with alternate, entire (rarely ciliate-serrulate), glabrous to tomentose, lepidote, or strigose leaves. Buds with several to many imbricate scales. Flowers pedicellate, usually in terminal corymbs [sometimes solitary or few, rarely from lateral buds]. Calyx 5-parted, various, often very small [rarely 6–10-parted], persistent. Corolla white to yellow, pink, purple or deep red, rotate to campanulate or funnelform [sometimes tubular], usually irregular, with a 5[rarely 6–10]-lobed limb [rarely some of the lobes divided to the base], the median lobe adaxial; deciduous. Stamens 5–7–10[–20], usually exserted from the corolla [except in some tropical montane groups], the filaments usually unequal, the anthers unappendaged, muticous, without white disintegration tissue, opening (through collapse tissue) by apical pores; pollen tetrads with viscin strands. Stigma capitate; style slender, curved; ovary 5[–10–20]-locular, superior, free from the calyx; ovules numerous in each locule. Fruit a septicidal capsule, usually ovoid to oblong; seeds numerous, minute, flat and more or less winged to fusiform [or caudate]. Basic chromosome number 13. (Including *Azalea* L. sensu Desv., *Azaleastrum* Rydb., *Biltia* Small, *Hymenanthes* Blume, *Rhodora* L.) LECTOTYPE SPECIES: *R. ferrugineum* L.; see N. L. Britton, N. Am. Trees 752. 1908. (Name from Greek, *rhodon*, rose, and *dendron*, tree; the ancient Greek name of *Nerium Oleander* L.) — RHODODENDRONS, AZALEAS.

A genus of 800 or more species of the colder and temperate parts of the Northern Hemisphere, centering in eastern and southeastern Asia, and especially the Himalayas, extending southward on the high mountains of Malaysia, the Philippines, and New Guinea to Queensland, and with a

much smaller center of development in eastern North America, a few species in the mountains of Europe, and *R. lapponicum* (L.) Wahlenb. (*2n* — *26*, *52*) circumboreal. About *21* species occur in continental North America, including 17 species in four sections in the southeastern United States.

Most authors with more than a regional viewpoint have maintained *Rhododendron* as a polymorphic genus difficult to divide into large, well-marked natural units and susceptible of only artificial division into genera of convenience. Both Copeland and Cox have proposed dismemberment of the inclusive genus on anatomical grounds, but very few (including almost none of the taxonomically critical) species have been examined in this respect. The subgeneric classification is still in a state of flux, and from four to eight subgenera and as many as 20 sections or some 43 informal "series" have been recognized. The conservative course of emphasizing morphological and genetic similarities, rather than differences, is followed here and the subgeneric categories are taxonomically those of Rehder. The species of the southeastern United States fall into four well-marked groups which have been placed in three genera (*Rhododendron*, *Biltia*, *Azalea*). The relationships of these are not directly with each other but with species elsewhere, and the much greater diversity of the Asiatic species bridges the discontinuities seen on a purely regional basis.

Subgenus RHODODENDRON (subg. *Eurhododendron* Drude) comprises evergreen [or rarely deciduous] species with flowers produced in terminal umbel-like racemes on shoots of the preceding year, the stamens 5–20. Two sections are represented in our area. Section PONTICUM G. Don (§ *Leiorhodium* Rehd.; *Hymenanthes* Blume) has glabrous to tomentose persistent leaves, [glabrous,] glandular or hairy ovaries, and 10–20 stamens. *Rhododendron catawbiense* Michx. and *R. maximum* L. (both *2n* = 26) occur in the eastern United States, the former largely in the southern Appalachians. Most closely related to *R. ponticum* L. (*2n* = 26), of Europe and Asia Minor, and to *R. macrophyllum* D. Don ex G. Don (*2n* = 26), of California to British Columbia, the two are distinctive morphologically (leaf shape, flower size and color, indument of ovary, etc.), ecologically, and seasonally, hybridizing occasionally (to produce *R.* × *wellesleyanum* Waterer ex Rehd.) when ecological and seasonal barriers break down. *Rhododendron catawbiense* is interfertile with a number of other species of the section and has been used extensively in the production of hardy ornamental hybrids.

Section RHODODENDRON (§ *Leipipherum* G. Don), with leaves and ovary lepidote with entire-margined, patelliform scales, and stamens 10, is represented by three closely related magenta- to white-flowered taxa (subsect. *Caroliniana* Sleumer) ranging entirely within our area. *Rhododendron carolinianum* Rehd. (*2n* = 26) occurs mostly at higher altitudes in the mountains of North Carolina, Tennessee, South Carolina, and northeastern Georgia. Although usually with pink or white corollas, a clear yellow form (f. *luteum* Frisbie) has been described from a cultivated plant presumably collected in western North Carolina. *Rhododendron minus*

FIG. 2. **Rhododendron**. a–e, *R. carolinianum*: a, flowering branchlet, × ½; b, flower, × ½; c, flower, lateral view, corolla and four stamens removed, × 1; d, ovary, cross section, semidiagrammatic, × 10; e, seed, hilum at lower end, ca. × 20. f–k, *R. Vaseyi*: f, inflorescence, × ½; g, flower, × ½; h, flower, lateral view, corolla and three stamens removed, × 1; i, branchlet with fruits of two seasons, flower buds and vegetative bud, × ½; j, capsule showing dehiscence by septicidal slits, × 1½; k, seed, hilum at lower end, ca. × 20. l–q, *R. atlanticum*: l, flowering branchlet, × ½; m, flower, × 1; n, anther, inner view, × 5; o, stigma, × 10; p, capsule, × 1½; q, seed, hilum at lower end, ca. × 20.

Michx. (*R. punctatum* Andr., *R. Cuthbertii* Small) ($2n = 26$) is a plant of lower altitudes, primarily in the Piedmont, in scattered localities from central Alabama to southwestern Georgia and northward to North Carolina, while *R. Chapmanii* Gray is of much more restricted distribution, occurring in scattered colonies in pinelands and on bluffs in the Apalachicola region of western Florida and in northeastern Florida. The latter two are similar in conformation of the corolla, while *R. minus* and *R. carolinianum* are similar in leaf shape and habit (although the former is a taller, more straggling and later flowering shrub than the latter). The three apparently are largely separated geographically and ecologically, although the ranges of *R. carolinianum* and *R. minus* seem to approach one another closely in northeastern Georgia and some intergradation may occur.

Subgenus ANTHODENDRON (Reichenb.) Rehd.[4] includes deciduous to evergreen species with the flowers in leafless corymbs at the ends of shoots of the previous season, the stamens 5–10. Four sections are recognized, two in our area, two entirely Asiatic. Section TSUTSUSI Sweet (§ *Tsutsutsi* G. Don) includes many of the commonly cultivated azaleas: *R. indicum* (L.) Sweet, *R. Simsii* Planch., *R. obtusum* (Lindl.) Planch., among others, as well as many artificial hybrids.

Section RHODORA (L.) G. Don, with flowers from a terminal bud, the leafy shoots from separate lateral buds and stamens 10 or 7, includes five species: three of Asia; *R. canadense* (L.) Torr. ($2n = 52$, and unique in the genus in the deeply divided corolla) entirely within the glaciated area to the north of our range; and *R. Vaseyi* Gray (*Biltia Vaseyi* (Gray) Small) ($2n = 26$), restricted to a limited area of western North Carolina at 900–1600 m. altitude. *Rhododendron Vaseyi* is quite distinct in the pale-pink, 2-lipped, rotate-campanulate corolla with very short tube, the uppermost corolla lobe exterior in the bud, and the stamens 7 (5 or 6), but, as Rehder (1926) has shown, *Biltia* Small cannot be maintained on these bases. The species is isolated among the American taxa and is probably most nearly related to the Japanese *R. Albrechtii* Maxim. Both species reportedly have been crossed with *R. Schlippenbachii* Maxim. (very similar in floral structure, but of the Asiatic sect. BRACHYCALYX Sweet

[4] Seithe-von Hoff (1960, p. 312) adopts subg. *Azalea* (L.) Planchon (Fl. des Serres 9: 75. 1853 54) as the correct name for this taxon, maintaining that Rehder (Jour. Arnold Arb. 2: 156–159. 1921) was incorrect in typifying *Azalea* L. by *A. procumbens* L. (*Loiseleuria procumbens* (L.) Desv.) and that *A. pontica* L. (*Rhododendron luteum* Sweet) should be selected instead as lectotype species. However, Rehder's arguments seem relevant, and, as he pointed out, *Azalea* was effectively typified by Salisbury who removed the other species to *Rhododendron*, leaving only *A. procumbens* in *Azalea*. Since this species is also the type of the conserved name *Loiseleuria*, *Azalea* L. is automatically unavailable. Planchon, moreover, published this combination as a section, rather than a subgenus. It is mentioned only briefly as "un sous-genre auquel nous réservons le nom sous-générique d'*Azalea*." However, sect. *Tsutsia* Planchon, which is clearly indicated on the following page as "*Rhododendron*, sect *Tsutsia*," receives similar treatment, Planchon noting that it is composed of the "Azalées de l'Inde, encore plus clairement un simple sous-genre du type *Rhododendron* pour lequel nous prosposerons le nom de *Tsutsia*." The parallel is clear, and "sous-genre" is to be translated as "sectio" in this instance.

[§ *Sciadorhodion* Rehd. & Wils.] in which the flowers are from terminal buds with leafy shoots from the axils of the lower scales of the same bud).

Section ANTHODENDRON (§ *Pentanthera* G. Don), with the inflorescence from the terminal bud and leaves from lateral buds below, stamens 5, leaves mostly deciduous, and pubescence, if present, setose or the hairs flattened, includes the European *R. luteum* Sweet (*R. flavum* G. Don), the Japanese *R. japonicum* (Gray) Suringar, the Chinese *R. molle* (Blume) G. Don, the western American *R. occidentale* (Torr. & Gray) Gray, and about 13 species centering in the southeastern United States but extending northward to New England, southern Quebec, central New York and westward to Arkansas and eastern Texas. The group includes the red- to yellow-flowered *R. Bakeri* (W. P. Lemmon & McKay) Hume (including *R. cumberlandense* E. L. Braun), *R. flammeum* (Michx.) Sarg. (*R. speciosum* Sweet), *R. calendulaceum* (Michx.) Torr., *R. austrinum* (Small) Rehd., and *R. prunifolium* (Small) Millais; the pink-tubed to pink-flowered *R. roseum* (Loisel.) Rehd., *R. nudiflorum* (L.) Torr., and *R. canescens* (Michx.) Sweet; and the essentially white-flowered *R. alabamense* Rehd., *R. atlanticum* (Ashe) Rehd., *R. viscosum* (L.) Torr., *R. serrulatum* (Small) Millais, *R. oblongifolium* (Small) Millais, and *R. arborescens* (Pursh) Torr. These basic species are distinctive, differing morphologically in characters of bud scales, corollas, leaves, and pubescence, but hybridization in many areas has so blurred the lines between species that precise identification of individual specimens is difficult or impossible. With the exception of *R. calendulaceum* ($2n = 52$), all are diploids ($2n = 26$) which produce largely fertile hybrids. However, considerable hybridization seems to have occurred between *R. calendulaceum* and diploid species; in most instances the hybrids are tetraploid. Differences in geographical distribution, ecology, and flowering time appear to be the chief barriers to hybridization, and wherever these overlap perplexing hybrid swarms, sometimes involving three or more species, may occur. Only the late-flowering and isolated *R. prunifolium*, of southwestern Georgia and adjacent Alabama, is not known to hybridize with other species in the wild, but *R.* × *gladwynense* M. G. Henry, its artificial hybrid with *R. serrulatum*, is fertile and vigorous. Other combinations of allopatric species also produce fertile hybrids, and *R.* × *gandavense* (K. Koch) Rehd. is noteworthy as a showy artificial hybrid swarm involving at least *R. luteum*, *R. calendulaceum*, and *R. nudiflorum* and probably *R. viscosum* and other species.

Chromosome numbers have been reported for about 360 species of *Rhododendron*. The species of subg. RHODODENDRON § PONTICUM, subg. AZALEASTRUM, and subg. ANTHODENDRON appear to be diploids ($2n = 26$), with the two exceptions noted above, but subg. RHODODENDRON § RHODODENDRON includes a number of series with varying degrees of polyploidy (about 44 known tetraploids, 22 hexaploids, 1 octoploid, 1 duodecaploid), apparently correlated with altitude in the high mountains of Asia. A large number of species are in cultivation, especially in the milder

climates of Great Britain and the northwestern United States, and many hybrids have been made both between closely related species and even those of different subgenera (e.g., RHODODENDRON × ANTHODENDRON = subg. × AZALEODENDRON). All of the intersubgeneric hybrids appear to be sterile, however, and some are weak or inviable. Self-compatibility to -incompatibility have been recorded for various species (e.g., *R. catawbiense*) and hybrids. The genus appears to be proterogynous throughout. The horticultural and technical literature on the genus is enormous.

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Tribe ANDROMEDEAE Endlicher

7. **Leucothoë** D. Don. Edinburgh New Philos. Jour. 17: 159. 1834.

Evergreen or deciduous shrubs (or small trees), with alternate, short-petioled, serrulate or crenulate to entire leaves; winter buds small, with several outer scales. Inflorescences racemose, from axillary buds on wood

of the preceding season; flowers in the axils of small, persistent bracts [in *L. Grayana* one or more flowers in the axils of leaves, the inflorescence terminating a short leafy branch of the same season from an axillary bud]; pedicels with two opposite bracteoles at the base or beneath the calyx. Calyx of 5 nearly distinct sepals imbricate or quincuncial in bud. Corolla ovoid or cylindric, glabrous, white [to red], with 5 short lobes. Stamens 10, on the base of the corolla; filaments straight or S-shaped, expanded at the base, glabrous to villous, unappendaged; anthers opening by pores, obtuse or 2- or 4-awned at the apex (the awns sometimes minute), with white disintegration tissue in the angle between the awns (or in this position when the awns are lacking); pollen tetrads without viscin strands. Stigma expanded, somewhat peltate and 5-lobed to truncate; style straight, included or exserted from the corolla; ovary superior, 5-locular; placentae undivided, at the top of the axis, with the anatropous to campylotropous ovules mostly pendulous on the outer and/or under side. Fruit a 5-lobed, depressed-globose capsule, 5-valved, loculicidal, without thickened sutures, the calyx and placentae persistent; seeds pendulous, scobiform, angled, with a loose, thin testa, sometimes winged. (Including *Eubotrys* Nutt., *Agarista* D. Don ex G. Don.) TYPE SPECIES: *L. axillaris* (Lam.) D. Don. (A poetic name, for Leucothoë, daughter of Orchamus, King of Babylon, mentioned by Ovid.)

A genus of about 50 species, variously placed in about six genera, two subgenera, or seven sections; about four species in eastern Asia, 35 in South America, one in Central America, one in California and Oregon, and five (in three sections) in the eastern United States.

Section LEUCOTHOË, composed of evergreen species with bracteoles at the base of the pedicels, erect, glabrous to short-pubescent filaments, and anthers with four very short (in ours) to long awns, is represented in the southeastern United States by two closely related species. *Leucothoë axillaris* (*L. Catesbaei* (Walt.) Gray, but not sensu Gray or most authors; *L. platyphylla* Small), with abruptly pointed leaves with petioles to about 1 cm. long and with rather broadly ovate or rounded bracts and sepals broadly ovate (hence still imbricate at anthesis), is confined to low woods on the Coastal Plain from Florida westward to Louisiana and northward to southeastern Virginia. *Leucothoë Fontanesiana* (Steud.) Sleum. (*Andromeda Fontanesiana* Steud., *L. editorum* Fern. & Schub., *L. Catesbaei* sensu most authors), with decidedly long-acuminate leaves, longer petioles, and the bracts lanceolate-acuminate, the sepals ovate-oblong and acutish (hence scarcely imbricate at anthesis), is a plant of cool, moist woods (especially along streams) in the mountains of southwestern Virginia, western North Carolina, eastern Tennessee, and northern Georgia. The two species, which appear to be completely isolated, are in need of further study, for, although the leaf shapes usually are distinctive, those of bracts and sepals appear to be less so. *Leucothoë Fontanesiana* is far hardier than *L. axillaris* and is important horticulturally northward to New England.

The closest relative of these two species is *L. Griffithiana* C. B. Clarke (including *L. tonkinensis* Dop), of Indochina, Burma, Yunnan, and southeastern Tibet. The placing of this species, which is amazingly similar to ours, in sect. OLIGARISTA Sleum. on the basis of the greater development of the four awns on the anthers unfortunately obscures another of the close relationships between species of Asia and North America. Other related species which fit well into sect. LEUCOTHOË are *L. Davisiae* Torr. (§ *Acranthes* Sleum.), of California and Oregon, and *L. Keiskei* Miq. (§ *Paraleucothoë* Nakai), of Japan.

Section AGASTIA DC. (*Agarista* D. Don ex G. Don), a distinct section of clearly related species in which the leaves are persistent and entire, the anthers without awns, the filaments S-curved and villose, the stigmas truncate, and the bracts and bractlets narrow, is primarily South American with its center of differentiation in Brazil. *Leucothoë mexicana* (Hemsl.) Small, ranges from Honduras to Mexico, and the similar *L. populifolia* (Lam.) Dippel (*L. acuminata* (Lam.) G. Don), $2n = 24$, occurs in swamps and low hammocks on the Coastal Plain from central Florida northward to South Carolina. Among our species, *L. populifolia* is easily recognized by the entire, lanceolate to ovate-lanceolate, persistent leaves, the loose racemes of long-pediceled white flowers in April or May, as well as by the other characters of the section.

Section EUBOTRYS (Nutt.) Gray (*Eubotrys* Nutt.) includes only two deciduous species of the eastern United States with axillary inflorescences developing the summer before flowering (as in *Cassandra* and *Pieris*), bracteoles on the pedicel just beneath the calyx, and anthers conspicuously 2- or 4-awned at the apex. One, *L. racemosa* (L.) Gray, with 4-awned anthers and wingless seeds, is a plant of the Coastal Plain from Massachusetts to Florida and eastern Texas. Within this species three varieties (*racemosa*, *elongata* (Small) Fern., and *projecta* Fern.) have been proposed on the basis of pubescence of branchlets, development of the inflorescence, and size of corolla. The other, *L. recurva* (Buckley) Gray, with recurved racemes, 2-awned anthers, and winged seeds, is a montane species, mostly of rocky, open woods with other Ericaceae, *Pinus*, and *Quercus*, from western Virginia to eastern Tennessee and northern Georgia. On the basis of floral anatomy and embryology these two species were the most primitive of the 22 of the Andromedeae studied by Palser. The exact relationship of these and *L. Grayana* Maxim. (§ *Eubotryoides* Nakai), of Japan, to the remainder of the genus is in need of thorough study.

Leucothoë is distinguished by the axillary racemes (those of *L. Grayana* terminating short, leafy branches from axillary buds of the preceding season), the imbricate sepals, the stamens with terminal awns (or these lacking), the white areas of disintegration tissue in the connective lobes extending to the base of the awns (or the position they should occupy if present), the lack of spurs on the filaments, the dry capsular fruit lacking thickened margins, and the seeds with loose seed coats, sometimes winged. The genus appears to be most closely related to *Gaultheria* (*q.v.*); when

awned, the stamens are strikingly like those of both *Gaultheria* and *Zenobia*.

The observations of Palser that "the species of *Leucothoë* have one character in common which separates them from other species studied — the position of the placentae against the outer carpel walls with the ovules borne on the inside surfaces," need to be extended, for other species do not conform. In *L. axillaris*, *L. Fontanesiana*, and *L. Davisiae* the stalked placentae extend along the top of the locule and bend downward, bearing ovules only on the lower, inner surface; and in *L. racemosa* and *L. recurva*, the placentae are like those of *Cassandra*: columnar with the end pressed against the ovary wall, the ovules borne around the margins. However, in *L. populifolia*, *L. Griffithiana*, and *L. Grayana*, the ovules are borne on the outer as well as lateral surfaces of the stalked placentae.

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8. **Gaultheria** Linnaeus, Sp. Pl. 1: 395. 1753; Gen. Pl. ed. 5. 187. 1754.

Dwarf, prostrate, evergreen undershrubs [to upright shrubs or rarely small trees] with broad, alternate [rarely opposite], short-petioled, usually serrate leaves; winter buds ovoid, with several outer scales. Flowers bisexual [or rarely both bisexual (?) and carpellate, the latter with much reduced stamens], 5(rarely 4)-merous, [in terminal panicles or axillary racemes or clusters or] in ours solitary in the axils of leaves; pedicels with 2 bractlets [at the base or middle or] immediately beneath the calyx [or the bracteoles several, scattered]. Calyx 5(4)-parted, [usually] accrescent and becoming fleshy. Corolla campanulate to urceolate, white to pink, glabrous or hairy within. Stamens 10 (8), on the base of the corolla; filaments expanded at the base, hairy or glabrous; anthers with white disintegration tissue on the abaxial side at the base of the bifid terminal awn on each anther-half [or in this position when awns are lacking], or disintegration tissue lacking in the most reduced species, the anthers opening by terminal pores; pollen tetrads without viscin strands. Stigma obtuse or truncate; style straight; ovary superior (and free from the calyx) or rarely partly inferior, 5(4)-locular, the axile placentae with 5–10[–many] ovules; disc 10-lobed. Fruit a 5(4)-valved loculicidal capsule inclosed by and rarely united with the usually colored (red, white [to bright blue or black]) and fleshy calyx, appearing berry-like; seeds usually numerous, small, hard, angled, wingless. (Including *Chiogenes* Salisb.) TYPE SPECIES: *G. procumbens* L. (Named in honor of Jean-François Gaulthier, ?1708–1756, botanist and court-physician at Quebec.)

A genus of perhaps 150 species, many of high mountains: in Asia ranging from Japan, China, and the Himalayas, southward to New Guinea, Australia, Tasmania (three species), and New Zealand (about six species); in North America from Labrador to British Columbia, southward through Mexico and the West Indies to Patagonia. *Gaultheria* has not been revised as a unit, but Airy-Shaw has placed the species of continental Asia in five sections which include the species of North America. Section GAULTHERIA (§ *Eugaultheria* Airy-Shaw) occurs in America as two widespread species primarily of the East; sects. AMBLYANDRA Airy-Shaw and BROSSAEOPSIS Airy-Shaw are represented in the West by *G. ovatifolia* Gray and *G. humifusa* (Graham) Rydb. and by *G. Shallon* Pursh, respectively. The two species of the West Indies and those of Central America also belong to sect. BROSSAEOPSIS.

Section GAULTHERIA (dwarf undershrubs with mostly small leaves and solitary flowers with two opposite bracteoles immediately beneath the calyx) includes the most reduced species in the genus. Series *Procumbentes* Airy-Shaw comprises only the pentamerous, red-fruited *G. procumbens* ($2n = 24$), nomenclaturally typical but morphologically an isolated type in the genus. Widespread in eastern North America (Newfoundland to Manitoba, south to Minnesota, Georgia and Alabama [in the mountains], and southeastern North Carolina), the species is prob-

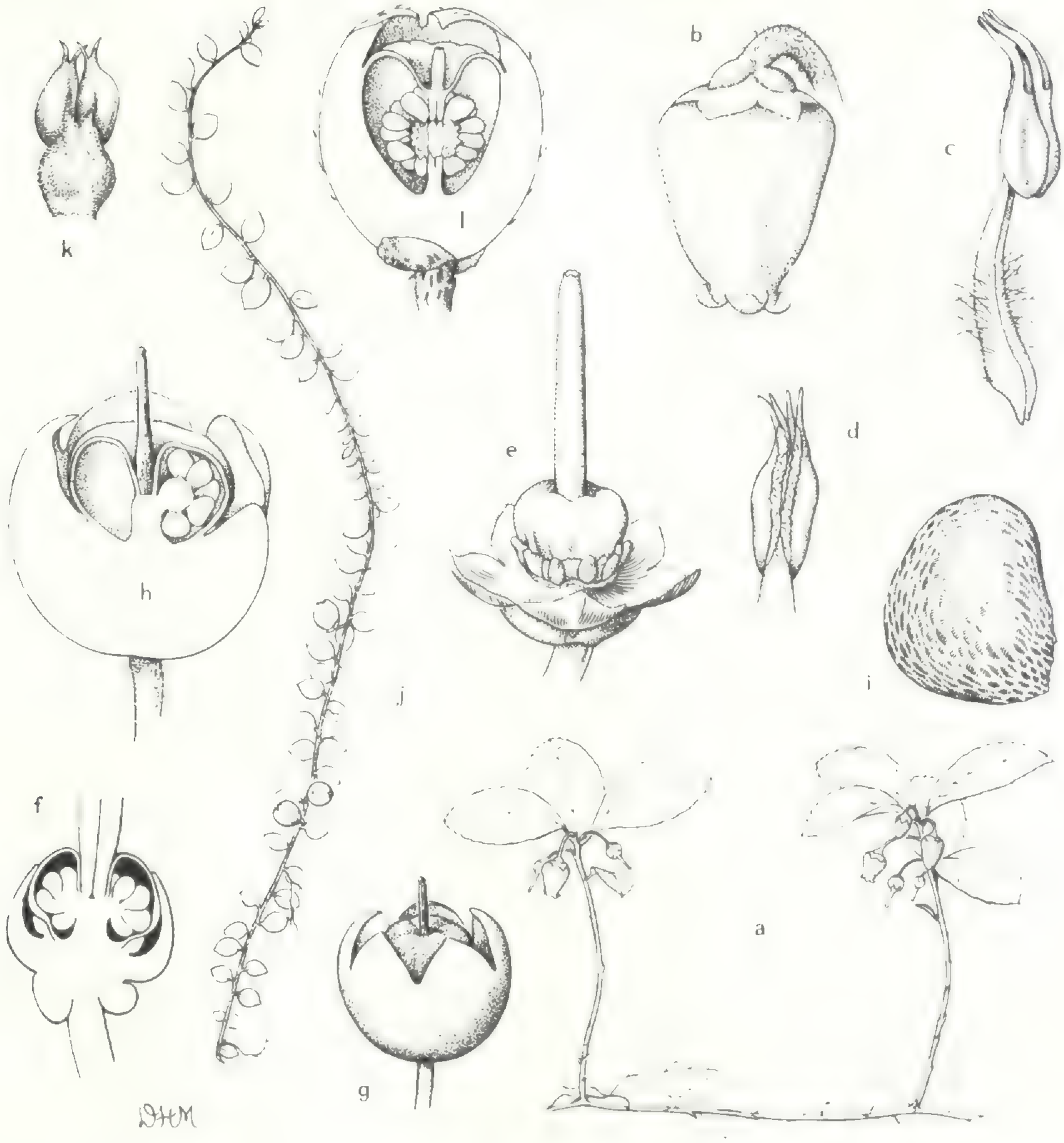

FIG. 3. **Gaultheria.** a–i, *G. procumbens*: a, habit, × ½; b, flower, × 3; c, stamen, × 10; d, anther, outer view, showing lines of disintegration tissue, awns, × 10; e, calyx, disc, gynoecium, × 6; f, ovary, disc, calyx, vertical section, × 6; g, fruit with accrescent calyx, × 2; h, fruit and calyx in vertical section, × 3; i, seed, × 20. j–l, *G. hispidula*: j, fruiting shoot, from below, × ½; k, stamen, outer view, showing lack of disintegration tissue, × 20; l, immature fruit in vertical section — note two calyx lobes at top, × 4.

ably most closely related to *G.* (§ *Leucothoides*) *pyroloides* Miq., of Japan. Series *Hispidulae* Airy-Shaw (which seems to have little relationship to *Procumbentes*) includes only two tetramerous-flowered, small-leaved, delicate, creeping species which represent "the last word in reduction in the genus." *Gaultheria hispidula* (L.) Muhl. var. *hispidula* (*Chiogenes hispidula* (L.) Torrey & Gray) is a white-fruited plant, mostly of cold woods and bogs to the north of our range (Labrador to New England and Pennsylvania, westward to Minnesota, Idaho, and British Columbia) but extends sporadically southward in cold mountain bogs to western North Carolina. Varietas *japonica* (Gray) Makino, of central and northern

Japan, differs only in the more obovate leaves with more cuneate base and in the shorter and less deeply bifid awns of the anthers. The second species, the awnless, red-fruited *G. suborbicularis* W. W. Sm., occurs in the high mountains of Yunnan. In both, the calyx tube enlarges into a berry-like structure which almost completely surrounds and is united with the capsule, while the calyx lobes persist almost unchanged at the top. The appearance thus given of a berry from an inferior ovary (in flower the ovary is about half-inferior) has led to the erroneous association of *G. hispidula* (as *Chiogenes*) with the Vaccinioideae. A third series, *Trichophyllae* Airy-Shaw, consists of eight or more pentamerous species, of the Sino-Himalayan ranges.

Closely related to (and perhaps congeneric with) *Gaultheria* is *Pernettya* Gaud. (Mexico to Patagonia, New Zealand, and Tasmania) which differs consistently only in the baccate (*vs.* capsular) fruit, although usually, but with exceptions in both genera, in the dry *vs.* fleshy calyx. Natural hybrids (× *Gaulthettya* Camp) have been found in New Zealand, Mexico, and the Falkland Islands. × *Gaulthettya wisleyensis* (Marchant) Rehd. (*G. Shallon* Pursh [$2n = 88$] × *P. mucronata* (L. f.) Spreng. [$2n = 66$]) is a heptaploid ($2n = 77$) which is partially fertile (presumably through pairing within the polyploid parental genomes?) producing aneuploid offspring (e.g., $2n = 70, 71, 79$). Such hybridization was suggested by Callan as a possible method of origin of new species; Camp suggested independently that the Mexican *P. ciliata* (Cham. & Schlecht.) Small and perhaps *P. hirsuta* (Mart. & Gal.) Camp may have resulted from a backcross between a × *Gaulthettya* and the *Pernettya* parent or from genetic segregation within the hybrid itself. A number of interspecific hybrids, some fertile, are known in *Gaultheria*. Base chromosome numbers of 11, 12, and 13 have been reported in *Gaultheria* ($2n = 22, 24, 26, 44, 88, 96$), and of 11 in *Pernettya* ($2n = 22, 44, 66$).

Gaultheria shows with other genera reticulate relationships which hardly support the retention of the tribe Gaultherieae as a natural unit apart from the Andromedeae. Airy-Shaw notes *G. codonantha* Airy-Shaw, from Assam, as nearest to the prototype of the genus, and indicates a close agreement "in the morphology of the calyx, corolla, filaments, anthers and seeds," as well as in the inflorescence, between this species and *Zenobia* and *Lyonia* § *Lyonia* and § *Maria*. He further calls attention to the resemblance of *G.* (§ *Leucothoides*) *Griffithiana* Wight to *Leucothoë Griffithiana* C. B. Clarke, remarking that the former provides an almost perfect link between *Gaultheria* and *Leucothoë* § *Leucothoë*. He would regard *Gaultheria* as an advanced type "adapted for seed-dispersal by the agency of birds."

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9. **Zenobia** D. Don, Edinburgh New Philos. Jour. 17: 158. 1834.

Deciduous to half-evergreen, glabrous, often glaucous shrubs with alternate, short-petioled serrulate-crenulate to entire, veiny, coriaceous leaves; buds ovoid, obtuse, with several outer scales. Flowers showy, nodding, fragrant, in corymbs from axillary buds on the upper part of twigs of the

preceding season; individual flowers in the axil of a short bract, the pedicel with 2 lateral bracteoles at the base. Calyx lobes 5, valvate, thickish, persistent and somewhat accrescent in fruit. Corolla white, broadly campanulate, obtusely 5-lobed. Stamens 10; filaments abruptly enlarged below, flattened; anthers opening by oblong pores, each anther-half surmounted by a pair of slender ascending awns and with a conspicuous area of white disintegration tissue in the connective; pollen tetrads without viscin strands. Stigma truncate, simple; style columnar, about as long as the corolla; ovary superior, 5-locular, 5-lobed, placentae from about the middle of the axis in each locule, with numerous ovules; disc 10-lobed. Fruit an erect depressed-globose loculicidal 5-valved capsule, the valves, axis, and placentae persistent; seeds numerous, angled, not winged. TYPE AND SOLE SPECIES: *Z. speciosa* (Michx.) D. Don = *Z. pulverulenta* (Bartr. ex Willd.) Pollard. (Name fanciful, for Zenobia, queen of Palmyra, 267–272 A. D., who conquered Egypt and most of Asia Minor.)

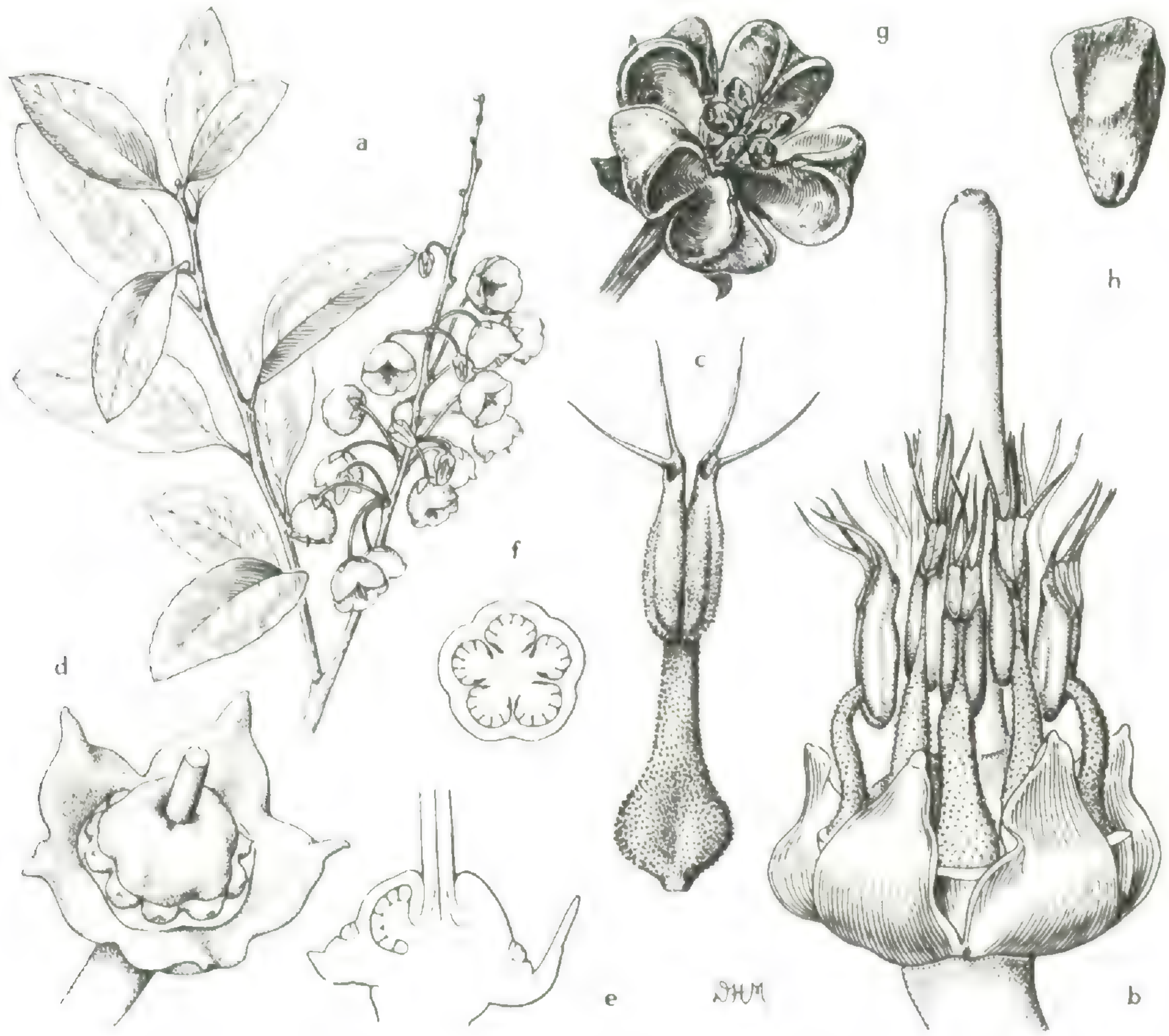

FIG. 4. **Zenobia.** a–h, *Z. pulverulenta*: a, flowering twig and new growth, × ½; b, flower with most of corolla removed — note white areas of disintegration tissue on back of each anther-half at base of awns, × 8; c, stamen, inner view, × 10; d, calyx, disc, and ovary, × 5; e, ovary and calyx in section, showing placentation and disc, semidiagrammatic, × 5; f, ovary, cross section, semidiagrammatic, × 5; g, open capsule, × 4; h, seed, × 15.

A single isolated species of damp, sandy or peaty, pine savannas, shrub-bogs, or swamp margins on the Coastal Plain from southeastern Virginia to northeastern South Carolina. *Zenobia pulverulenta* is a showy shrub with racemes of (1–)5–10-flowered corymbs of fragrant, campanulate, white flowers about 1.5 cm. across borne from May to mid-June. In f. *pulverulenta* the undersides of the leaves (in addition to stems, pedicels, calyces, and ovaries) are heavily glaucous, while in f. *nitida* (Michx.) Fern. (*Z. cassinefolia* (Vent.) Pollard; *Z. speciosa* (Michx.) D. Don. var. *nitida* (Michx.) Rehd.) the leaves are green beneath. Although the two have been treated as separate species, they occur together, along with intermediates, and there is no question that only a series of forms of a single distinctive species is represented. Both are showy but not often cultivated plants which are quite hardy at least as far north as Massachusetts.

Zenobia is characterized by the combination of inflorescence, 4-awned stamens, relatively large campanulate corollas, capsular fruit, and angled, unwinged seeds. There seem to be no close relatives, but the placentation and inflorescence resemble *Lyonia* § *Maria* while the corolla and stamens are reminiscent of *Gaultheria codonantha*, suggesting interrelationships with these genera. (See *Gaultheria*.) Neither the chromosome number nor observations on the biology of the plant seem to have been recorded.

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10. **Lyonia** Nuttall, Gen. N. Am. Pl. 1: 266. 1818, nom. cons.

Evergreen or deciduous shrubs [rarely small trees], with terete or angled branches. Leaves alternate, short-petioled, entire or shallowly toothed or serrulate, glabrous, or with hairs or peltate scales; winter buds ovoid, with 2 outer scales. Inflorescences axillary (sometimes appearing to be terminal, but falsely so), corymbose, [racemose] or paniculate, the racemes sometimes contracted into axillary clusters; each flower in the axil of a small leaf or bract and with 2 lateral bracteoles at the base of the pedicel, these sometimes quickly deciduous. Calyx 5(rarely 4–8)-lobed, the lobes valvate or reduplicate in bud, persistent or rarely deciduous in fruit.

Corolla cylindric-campanulate to urceolate or globose-urceolate, with 5(4–8) short lobes, white to pink, glabrous to hairy or lepidote. Stamens 10 (rarely 8–16); filaments flattened, often S-shaped, glabrous to hairy or roughened, with or without a pair of short, spurlike appendages on the back near the apex; anthers obtuse, the lobes parallel, lacking apical awns, dehiscent by large terminal pores, always with a white line of disintegration tissue on the back of each lobe extending at least along the apex of the filament and along the upper edge of the appendages when present; pollen tetrads without viscin strands. Stigma truncate to capitate; style columnar to fusiform, straight, not exserted; ovary superior, 5-locular, the placentae large, undivided; disc an enlargement of the ovary wall, variously developed. Capsule subglobose to ovoid, 5-angled, loculicidal, with paler, thickened sutures which may separate from the 5 valves in dehiscence; placentae persistent at the top of the columella; seeds scobiform, with a loose, thin testa. (*Xolisma* Raf.; not *Lyonia* Raf., 1808, or *Lyonia* Ell., 1817, nomina rejicienda; including *Arsenococcus* Small, *Desmothamnus* Small, *Neopieris* Britton.) LECTOTYPE SPECIES: *L. ferruginea* (Walt.) Nutt.; see I.C.B.N. 261. 1956, and Rickett & Stafleu, Taxon 9: 75. 1960. (In commemoration of John Lyon, 17?–1818, early American botanist and explorer of the southern Appalachians, "who fell victim to a dangerous epidemic amidst those savage and romantic mountains which had so often been the theatre of his labours.")

A genus of perhaps 40–50 species, in three or four sections, about ten in Asia (Kashmir to Japan, south to Malaya), perhaps 30 or more in the Greater Antilles, one or two in eastern and southern Mexico, and five in the United States. The Asiatic species belong to sect. PIERIDOPSIS (Rehd.) Airy-Shaw, with 1-sided, usually elongated racemes, filaments with or without appendages; leaves entire, persistent or deciduous), which might well be merged with sect. MARIA. Although the genus has been divided into a number of genera, the distribution of the characters used is so reticulate, when all of the species are considered, that segregates are essentially based on single-character differences. The species of the southeastern United States are distinctive, but the genus as a whole (especially § LYONIA) is in need of a thorough monographic study. Section MARIA (DC.) C. E. Wood[3] (*Xolisma* § *Maria* (DC.) Rehd.), as defined here, includes only three isolated species which are placed together on the basis of the filaments appendaged near the summit, the nonlepidote pubescence, and the

[3] The proper combination under *Lyonia* does not appear to have been made previously for this section. This combination, with additional synonymy is:

Lyonia Nutt. sect. **Maria** (DC.), comb. nov. Leucothoë D. Don, sect. *Maria* DC. Prodr. 7(2): 602. 1839; *Andromeda* L. sect. *Maria* (DC.) Gray, Man. Bot. North. U. S. 266. 1848; *Pieris* sect. *Maria* (DC.) Benth. & Hook. Gen. Pl. 2: 588. 1876; *Lyonia* subgen. *Maria* (DC.) Drude, Nat. Pflanzenfam. IV. 1: 44. 1889; *Xolisma* Raf. sect. *Maria* (DC.) Rehd. Jour. Arnold Arb. 5: 55. 1924; *Arsenococcus* Small in Small & Carter, Fl. Lancaster Co. 218. 1913; *Xolisma* Raf. sect. *Arsenococcus* (Small) Rehd. Jour. Arnold Arb. 5: 54. 1924. TYPE SPECIES: ***Lyonia mariana*** (L.) D. Don.

axillary corymbose (fasciculate) inflorescences. *Lyonia mariana* (L.) D. Don (*Neopieris mariana* (L.) Britton), $2n = 24$, ranging mostly on the Coastal Plain from Florida to Missouri, Arkansas, and eastern Texas, and

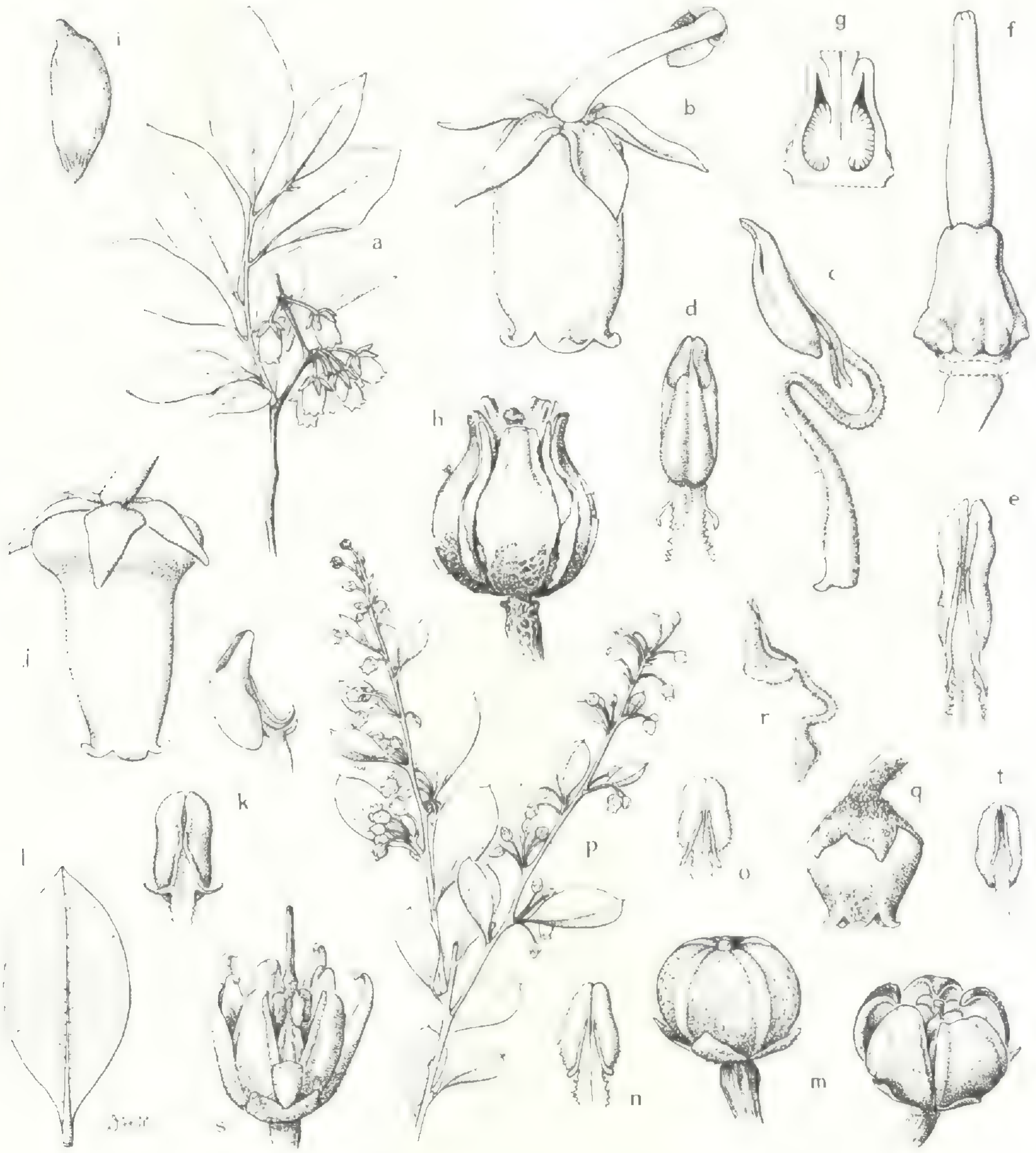

FIG. 5. **Lyonia.** a–i, *L. mariana*: a, branchlet, × ½; b, flower with bract and bractlets, × 3; c–e, lateral, inner and outer views of stamen and anthers to show filament appendages, disintegration tissue and anther dehiscence, × 10; f, gynoecium, lateral view — note glandular development of base of ovary, × 5; g, ovary, vertical section, semidiagrammatic, × 5; h, opened capsule — note partial separation of thickened valve-margins (carpel midribs), × 4; i, seed, × 20. j–l, *L. lucida*: j, flower, × 3; k, lateral and outer views of anthers — note appendages with margin of disintegration tissue, × 10; l, leaf, to show marginal vein, × ½. m–o, *L. ligustrina*: m, immature and opened capsules — note separation of differentiated margins, × 4; n, o, outer view of anthers of two collections to show appendages. p–s, *L. fruticosa*: p, flowering branchlet, × ½; q, flower, × 3; r, stamen, lateral view, × 10; s, opened capsule, one differentiated midrib (valve-margin) partially removed, × 4. t, *L. ferruginea*: outer view of anther, showing lines of disintegration tissue, × 10.

northward to eastern Pennsylvania, New Jersey, and southern Rhode Island, is notable for the calyx lobes deciduous with the leaves in fall, while *L. lucida* (Lam.) K. Koch (*Desmothamnus lucidus* (Lam.) Small, *Neopieris nitida* (Bartr.) Britton), $2n = 24$, distributed from western Cuba northward on the Coastal Plain to southeastern Virginia and Louisiana, is unique in the shining, persistent, coriaceous leaves with an intramarginal vein. Although *L. ligustrina* (L.) DC. is unique in the genus in the axillary or pseudoterminal inflorescences which are small panicles (racemes of corymbose fascicles) aggregated near the end of the growth of the preceding year, its separation as a monotypic section is doubtfully justifiable.[6] Within the broad range of this species (New England to New York, West Virginia, Kentucky, Arkansas, Oklahoma, and eastern Texas southeastward to Florida) a number of not very sharply limited geographical varieties in need of further study have been defined: vars. *ligustrina*; *salicifolia* (Wats.) DC.; *capreaefolia* (Wats.) DC.; *foliosiflora* (Michx.) Fern.; and *pubescens* (Gray) Bean (*Arsenococcus frondosus* (Pursh) Small).

Section LYONIA (*Xolisma* Raf.), with the flowers in dense axillary fascicles (as in § MARIA), the filaments unappendaged, the leaves persistent and lepidote, and the thickened part of the sutures separating as a whole from the rest of the capsule (sometimes seen in other sections as well), is primarily of the Greater Antilles, with two species, *L. ferruginea* (Walt.) Nutt. and *L. fruticosa* (Michx.) G. S. Torrey on the Coastal Plain from Florida to South Carolina. *Lyonia ferruginea* also occurs in Mexico along the eastern Sierra Madre from San Luis Potosí south to Oaxaca. The former is a shrub or small tree with leaves much rolled on the margin, while the latter is always a shrub of stricter habit with nonrevolute leaves and flowers as much as two months later.

Matthews and Knox (1926) and Anthony (1927) have doubted that any real distinction exists between appendages on the back of the anthers (spurs) and those at the summit of the filament (used by Rehder [1924] in separating *Pieris* and *Lyonia*). Their contention as to the lack of a real difference in the position of the appendages in these genera may be quite correct, but the appendages are not to be confused, for Palser has shown that those of *Pieris* lack the white disintegration tissue which is always present on the upper margin of the appendages of *Lyonia*.[7] Some

[6] The additional difference of a supposed absence of appendages on the filaments of this species does not hold, for short spurs which are comparable with those of *L. lucida* and *L. mariana* are present in this species. (See FIG. 5, *n*, *o*.) Palser (1951, p. 461) wrote, "Very short downward and laterally projecting spurs formed largely of tissue which disintegrates, arise from the filament below its point of attachment with the anther . . . The disintegrating areas continue upward. These spurs are observable only on young filaments, as they have disintegrated completely on mature ones and only the ragged lateral margins of the filaments remain." These appendages are clearly present in boiled-up flowers of the material which I have examined.

[7] Even when the filaments of *Lyonia* lack the awnlike appendages near the summit, a line of white disintegration tissue is present on each anther-halt, in some species of § LYONIA forming an inverted "V" at the junction of filament and anther. (See also footnote 6.) Confusion of the two types of appendages may have come in

of the other anatomical distinctions made by Palser (e.g., vertically *vs.* horizontally S-shaped filaments) do not hold, but the conspicuously paler, usually thickened sutures of the fruit, exclusively axillary inflorescences from the wood of the preceding season, two bracteoles at the base of the pedicels, and two large outer scales of the winter buds set *Lyonia* off as a natural group of species quite distinct from *Pieris*.

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11. **Pieris** D. Don, Edinburgh New Philos. Jour. **17**: 159. 1834.

Evergreen shrubs [small trees] rarely vines, with alternate [rarely opposite], short-petioled, coriaceous, broad, entire, crenulate, or toothed leaves; winter buds ovoid, with several narrow outer scales. Flowers white, in terminal panicles or axillary racemes produced the preceding summer, or racemes from axillary buds of the preceding growing season; pedicels each in the axil of a bract and with 2 alternate to opposite brac-

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part from the stamens of *Pieris bracteata* W. W. Sm. which were used as an example of both awned and appendaged anthers by Matthews & Knox and by Anthony. The plant has been found by Airy-Shaw to be not a *Pieris* but a form of *Vaccinium Forrestii* Diels (or a closely related species) with foliaceous bracts (Bot. Mag. **160**: *pl. 9490*. 1937).

teoles from above the base to beneath the calyx. Calyx deeply 5-lobed, the firm, thick-edged, ovate lobes valvate in bud, persistent in fruit. Corolla ovoid-urceolate to ovoid, with 5 short lobes. Stamens 10, included; filaments more or less vertically S-shaped and flattened; anthers with a pair of stout, deflexed spurs (without disintegration tissue) on the back just above junction with filament, otherwise unappendaged but with white disintegration tissue on the abaxial side of each of the often divergent anther-halves, each anther-half opening by a large oval to V-shaped pore; pollen tetrads without viscin strands. Stigma flat; style straight, as long as the corolla; ovary superior, 5-lobed, 5-locular, each locule with a short-stalked, pendent placenta on the axis near the top of the locule, the outer, lateral and lower surfaces with pendulous ovules; disc 10-lobed, with nectariferous lobes extending upward between the filaments. Capsule subglobose, loculicidally 5-valved, the sutures not thickened; seeds scobiform, nearly all pendulous, with a loose, cellular coat. (Including *Ampelothamnus* Small, *Arcterica* Coville.) TYPE SPECIES: *P. formosa* (Wall.) D. Don. (Name poetic, for *Pieris*, a Muse.)

A small genus of about eight species, five in eastern Asia, one in western Cuba, and two in the southeastern United States. *Pieris floribunda* (Pursh) Benth. (*Andromeda floribunda* Pursh) is a handsome shrub (to about 1.5 m.) of moist to dry, more or less open, rocky woods and mountain slopes from Virginia and eastern West Virginia to northern Georgia, eastern Tennessee, and Alabama. The inflorescences terminate the growth of the season in June or July; the small white flowers expand the following April or May. Although without any very close relatives, *P. floribunda* appears to be related to *P. japonica* (Thunb.) G. Don ($2n = 24$), *P. formosa* (Wall.) D. Don ($2n = 24$), *P. taiwanensis* Hayata, and *P. Swinhoei* Hemsl., all of Asia. *Pieris floribunda* and *P. japonica* are two of the best of the ornamental Ericaceae for the eastern United States.

Pieris phillyreifolia (Hook.) DC. (*Ampelothamnus phillyreifolia* (Hook.) Small), is a curious plant of cypress ponds, sphagnum bogs, or wet pinelands from southernmost Georgia to central Florida, western Florida, and southern Alabama, in which the inflorescences are axillary and apparently produced just prior to flowering (January to March). The plant, which may be a shrub to about 1 m. tall, may climb to 10 m. as a vine by growing beneath the outer bark of *Taxodium ascendens* Brongn. and sending out leafy stems at intervals. No rootlets or other organs of support are formed, and the species seems to climb only this *Taxodium*, in which the outer bark is composed of long, parallel, easily separable fibers. Although segregated as *Ampelothamnus* Small, largely on the basis of the axillary racemes and the strongly S-shaped flattish filaments, this species belongs in *Pieris*. The details of floral anatomy and the characteristic anthers are precisely those of *Pieris*, the flattening and curving of the filaments are only a matter of degree, and *P. cubensis* (Griseb.) Small, of Pinar del Río, an undoubted member of the genus, seems also to have

exclusively axillary racemes. The production of a number of deciduous scale-leaves on the lower part of the new growth, although seldom seen in *P. floribunda*, is well developed in *P. phillyreifolia* and is a characteristic pattern in *P. japonica* and its close allies.

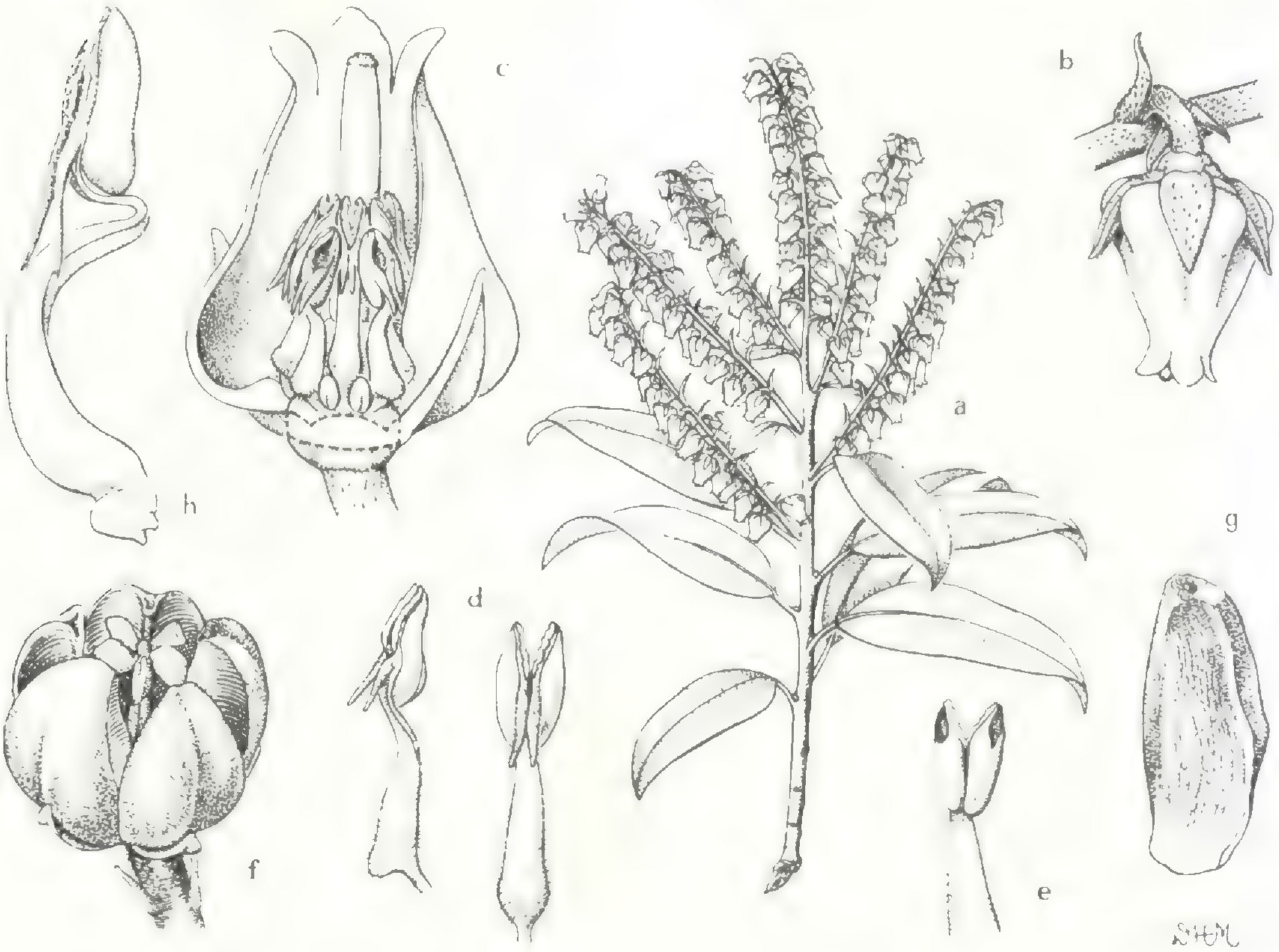

FIG. 6. **Pieris.** a–g, *P. floribunda*: a, flowering branchlet, × ½; b, flower, × 3; c, flower with half of corolla and calyx removed — note nectariferous lobes of disc between stamens, × 6; d, outer views of stamens from outer (left) and inner staminal whorls — note disintegration tissue along each anther-half above spurs, × 10; e, inner view of stamen from inner staminal whorl to show pores, edge of disintegration tissue on each anther-half, × 10; f, capsule, × 4; g, seed, × 10. h, *P. phillyreifolia*: stamen from outer staminal whorl, × 10.

The limits of *Pieris* have been a source of great confusion (see *Lyonia*), but the genus seems to be a natural unit consisting of evergreen species with persistent, coriaceous, serrulate, undulate, or bristle-margined leaves; winter buds with several narrow outer scales; racemose inflorescences either aggregated into terminal panicles or from the upper leaf axils; pedicels with bracteoles above the base; valvate sepals with fiber strands; anthers with stout deflexed spurs lacking disintegration tissue but with disintegration tissue in the connective above; and capsules without thickened or otherwise differentiated margins. The appendaged anthers are very distinctive and are in no way to be confused with those of *Lyonia*.

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12. **Cassandra** D. Don, Edinburgh New Philos. Jour. 17: 158. 1834.

Low, evergreen shrubs of sphagnum bogs, peaty swales, and pond margins. Leaves alternate, elliptic to lanceolate, short-petioled, entire or crenulate, more or less appressed to the stem; buds small, with several outer scales; vegetative parts, pedicels, and calyx (especially underside of leaves) scurfy with peltate scales. Flowers small, white, nodding, short-pediceled, solitary in the axils of the small upper leaves, forming almost horizontal, apparently 1-sided, 10–30-flowered, leafy racemes. Calyx small, 5-lobed, subtended by 2 persistent bractlets, aestivation quincuncial. Corolla oblong-urceolate, with 5 short lobes. Stamens 10, included; filaments flat, tapering upward; anthers terminating in 2 elongated tubes opening by a terminal pore, each sometimes prolonged beyond the pore as a minute triangular awn, otherwise unappendaged, lacking white disintegration tissue; pollen tetrads without viscin strands. Stigma slightly expanded; style straight, exserted from the corolla; ovary superior, 5-lobed, 5-locular, the placentae columnar, undivided, 1 in each locule from the center of the axis, the end flattened against the ovary wall, bearing about 15 campylotropous ovules around the edge; disc dark green, 10-lobed, nectariferous. Capsule depressed-globose, with slightly thickened sutures, loculicidally 5-valved, but the wall splitting into 2 layers, the inner 10-valved; seeds about 10 in each locule, small, somewhat compressed laterally, brown, shining, wingless. (Not *Cassandra* Spach, 1840. — *Leucothoë*; *Chamaedaphne* Moench, Meth. Pl. 457. 1794; not *Chamaedaphne* Mitchell, Diss. Brevis Principiis Bot. Zool. 1769 [= *Mitchella* L.].[8]) TYPE AND SOLE

[8] ***Chamaedaphne*** Moench (1794) is clearly a later homonym of *Chamaedaphne* Mitchell, first published in 1748 and taken by Linnaeus as the basis for *Mitchella* L. (1753) but republished validly in 1769. The earliest legitimate name appears to be

SPECIES: *Andromeda calyculata* L. = *Cassandra calyculata* (L.) D. Don. (A poetic name, for Cassandra, a daughter of Priam, King of Troy, and Hecuba.)

Cassandra calyculata (*Chamaedaphne calyculata* (L.) Moench) is of almost circumpolar distribution, ranging from Scandinavia, the Baltic States and northern Poland to northern Russia and northern Asia, Kamchatka, Manchuria, and northern Japan; and from Alaska to Labrador and Newfoundland, southward to British Columbia, Alberta, Minnesota, the northern parts of Illinois, Indiana, and Ohio, New York, Pennsylvania, and New Jersey, and southward in more or less isolated localities, mostly on the Coastal Plain, in Delaware, Maryland, North Carolina (there also inland in Henderson County), and South Carolina. Three geographical varieties have been distinguished: var. *calyculata* in Eurasia; var. *angustifolia* (Ait.) Rehd., the too similar widespread American form; and var. *latifolia* (Ait.) Fern., a dwarfish broad-leaved form of Labrador, Newfoundland, and Nova Scotia, westward in the north to Mackenzie.

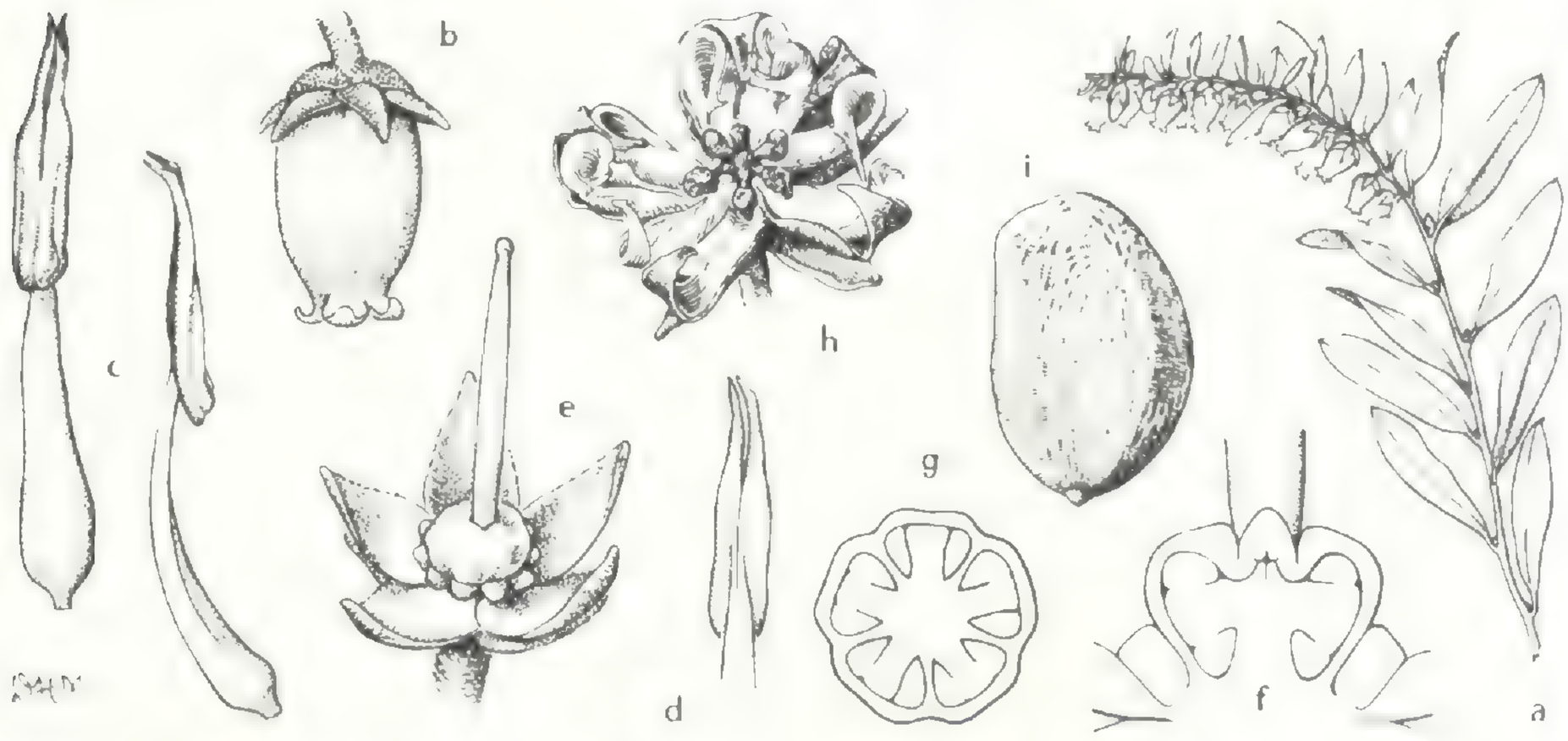

FIG. 7. **Cassandra.** a–i, *C. calyculata*: a, flowering twig, × ½; b, flower, × 3; c, inner and lateral views of stamens, × 10; d, outer view of anther, × 10; e, calyx and gynoecium with disc, × 6; f, ovary, disc, petals in diagrammatic vertical section — note columnar placentae, peripheral ovules, × 15; g, ovary, diagrammatic cross section, × 15; h, opened capsule — note five outer, ten inner valves, × 5; i, seed, raphe to left, × 20.

A low (exceptionally to 1.5 m.) and much-branched evergreen shrub with coriaceous, scurfy leaves, *Cassandra* is one of the most abundant and characteristic plants of bogs in the glaciated portions of eastern North

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Cassandra D. Don (1834) by which this plant was known to botanists of the nineteenth century. Although conservation may be advocated by some, such a course seems hardly justifiable for this single species, the list of *nomina generica conservanda* being already too cluttered with favorite "names my professor taught me," rather than consisting only of those of real consequence. It is not inappropriate, moreover, that *Cassandra* should be returned to the company of *Andromeda*, *Cassiope*, *Leucothoë*, *Phyllodoce*, *Pieris*, and *Zenobia*. See, however, M. L. Fernald's comments on the intrusion of *Harrimanella* upon this classic bevy (pages 28, 29, in "Some Historical Aspects of Plant Taxonomy," Rhodora **44**: 21–43. 1942).

America. It shows a wide tolerance, being an early invader of bogs, but often persisting long after the establishment of tree species. In some bog areas the plant is completely dominant, forming a closed association with *Sphagnum* and several other mosses. South of the glacial boundary, with the exception of southern New Jersey, the colonies appear to be rare and scattered.

The horizontal inflorescences terminate the growth of the year, and flower buds develop in late summer; the plants flower from March in the South to early July in Labrador; a partial second flowering sometimes occurs in the fall. The reduced leaves of the inflorescence are deciduous after maturity of the fruit (that portion of the shoot then dying) but the larger leaves below persist another year. Growth of the shoot is continued after flowering by one or more axillary buds below the inflorescence. The small, brown seeds have a large raphe of spongy tissue and appear to be capable of floating. The roots have been reported to lack mycorrhizae under bog conditions but to show such an association under drier conditions in cultivation. The leaves are poisonous, containing andromedotoxin.

Cassandra is a well-marked and apparently isolated genus distinctive in the bracteoles beneath the calyx, the stamens, the inflorescence, peltate scales, fruit, and seeds. The closest relationship seems to be with *Andromeda*, *Pieris*, and *Lyonia*.

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13. **Oxydendrum** A. P. de Candolle, Prodr. 7: 601. 1839.

A deciduous tree to 25 m., with a tall, straight trunk to 25–50 cm. in diameter, the bark deeply fissured. Winter buds small, axillary. Leaves membranaceous, oblong-lanceolate, petiolate, serrulate, pale beneath (remi-

niscent of *Prunus Persica*). Flowers bisexual, 6–8 mm. long, in drooping panicles (terminating the growth of the year) of 6 or more slender, declined racemes, these 1-sided (by the bending of the pedicels); each flower in the axil of a minute, deciduous bract, each pedicel with 2 minute, alternate, persistent bractlets. Calyx deeply divided into 5 separated lobes, valvate in bud. Corolla white, cylindric-ovoid to ovoid, puberulous, with 5 short, spreading or recurved lobes imbricate in bud. Stamens 10, hypogynous, free from the corolla; filaments broad, stout, swollen at the base; anthers appressed to the style, fixed near the base, linear-oblong, opening from the apex to above the middle by slitlike pores, the connective near anther apex with a region of white disintegration tissue; pollen tetrads without viscin strands. Stigma simple, unexpanded; style columnar, straight, slightly exserted; ovary superior, 5-locular, extending upward around the base of the style; ovules numerous on outer, lateral and upper surfaces of the conspicuous placentae, all near bottom of locule and extending upward. Pedicels recurving in fruit, the ovoid-pyramidal capsule erect, ca. 5 mm. long, crowned by the persistent style, loculicidally 5-valved; seeds numerous, elongate, ascending, the seed-coat pointed at the ends; embryo minute. TYPE AND SOLE SPECIES: *O. arboreum* (L.) DC. (*Andromeda arborea* L.). (Name from Greek, *oxys*, sour, and *den-*

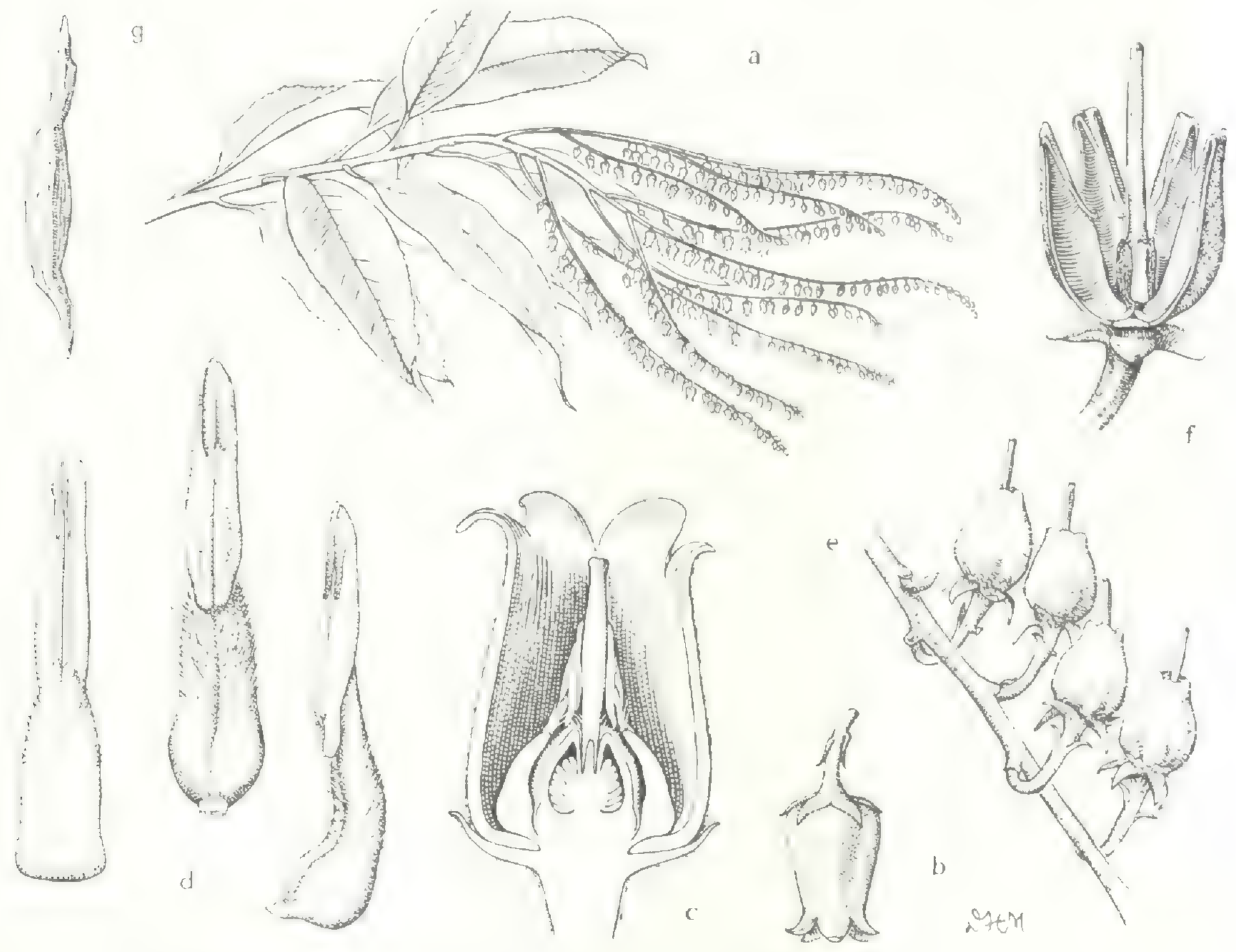

FIG. 8. **Oxydendrum.** a–g, *O. arboreum*: a, flowering branch, × ¼; b, flower, × 2; c, flower, in section, × 6; d, outer, inner, and lateral views of stamens — note area of disintegration tissue on upper part of outer surface of each anther-half, × 12; e, portion of raceme with immature fruits, × 2; f, opened capsule, one valve removed — note deeply immersed style, × 4; g, seed, × 10.

dron, tree, referring to the acid taste of the leaves.) — SOURWOOD, TITI, SORREL-TREE.

Oxydendrum arboreum is of wide distribution in the eastern United States in acid, well-drained soils in dry woods, on bluffs and ridges, in hammocks and creek bottoms, from southern Pennsylvania to northern and western Florida and to southern Ohio, southern Indiana and Illinois, and Mississippi and southeastern Louisiana. One of the largest of the Ericaceae, it is a handsome, slow-growing tree of great ornamental value both for its panicles of small, white flowers in June or July and for the showy red autumn coloration. It reaches its greatest size on the western slopes of the Smoky Mountains of eastern Tennessee. The plant is easily raised from seeds and transplants easily. It is hardy northward at least to eastern Massachusetts.

The species is an isolated one among the Ericaceae, apparently with no close relatives. Largely on the basis of the rather advanced evolutionary level of the wood anatomy in comparison with other members of the Andromedeae, Cox concluded that *Oxydendrum* is "the survivor of a comparatively long evolutionary sequence paralleling that of the other tribes," and placed it in a separate tribe, Oxydendreae. It is anatomically notable for the tapered receptacle with traces to all floral organs completely distinct.

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14. **Epigaea** Linnaeus, Sp. Pl. 1: 395. 1753; Gen. Pl. ed. 5. 186. 1754.

Prostrate evergreen shrubs with creeping stems. Leaves alternate, oval to elliptic, petiolate, coriaceous. Plants functionally dioecious (at least in *E. repens*), the flowers in short terminal and axillary bracteate spikes, the pedicels with 2 bractlets at the base. Flowers either carpellate (with rudimentary stamens, usually only filaments) or apparently bisexual, but with unexpanded stigmas and functionally staminate. Sepals 5, imbricate, conspicuous, green. Corolla salverform, with 5 spreading [or recurved] lobes, in staminate flowers about 1/3 larger than in carpellate. Stamens

of staminate flowers 10; filaments adnate to the base of corolla tube, half as long to as long as corolla tube; anthers elongate, the halves joined almost to the tip, lacking white disintegration tissue, opening by longitudinal slits (those of carpellate flowers, when present, not opening); pollen tetrads with viscin strands. Stigma 5-lobed, radiate and glandular in carpellate flowers, the lobes erect and dry in staminate flowers; styles half as long to as long as corolla tube; ovary superior, 5-locular, glandular-hairy; placentae 2 in each locule, axile below but parietal above (cf. Pyroleae, Monotropeae) with numerous anatropous ovules. Capsule depressed-globose, fleshy, glandular, hirsute, loculicidal, the valves thin; seeds numerous, minute, hard, brown, shining, on white, succulent placentae filling the locules. TYPE SPECIES: *E. repens* L. (Name from Greek, *epi*, on, and *gaea*, earth, in allusion to the creeping habit.) — TRAILING ARBUTUS.

Two species, *Epigaea repens*, of wide distribution in eastern North America (Labrador to northern Florida, Alabama, Tennessee, Indiana, Michigan, Minnesota, and Saskatchewan), and *E. asiatica* Maxim., of Japan to Formosa. Although closely related, *E. asiatica* differs from *E. repens* in the more acute, coriaceous leaves, the longer pedicels (to 1.5 cm. *vs.* 5 mm.), the greater number to flowers per inflorescence, the broader corolla tube and shorter lobes, and other details. *Epigaea* appears to be most closely related to the monotypic *Orphanidesia* Boiss., of the mountains inland from the southeast corner of the Black Sea, a similar low evergreen with 1–3 flowered racemes and a larger, cup-shaped corolla, but with anthers opening as in *Epigaea*. Within the Andromedeae both genera seem to be isolated, although, on the basis of wood structure, Cox placed *Epigaea*, *Agauria*, *Cassiope*, and *Enkianthus* together as Cassiopeae Cox.

Epigaea repens is noteworthy for its functional dioecism, the plants bearing either carpellate flowers with only rudimentary stamens (usually only the filaments developed) or seemingly bisexual but functionally staminate flowers with well-developed stamens and apparently functional embryo sacs, but stigmas which are not receptive to pollen. Although filament and style length vary, pollen grains are of a single size, and experimental evidence is all against any form of heterostyly. *Epigaea asiatica* does not appear to have been studied in this respect, but two artificial hybrids with *E. repens* (one a backcross to *E. repens*), both were of the pistillate type.

The roots do not develop root hairs, and a mycorrhizal association is obligate; as a result, the species transplants with difficulty. Although the plant seems to tolerate a fairly wide range of moisture and soil acidity (pH 7.6–4.5), constant moisture, good drainage, some shade, and acid soil apparently are required for optimum growth. The plant was formerly gathered in large quantities for the fragrant pink to white flowers produced in earliest spring, and has been very nearly exterminated in some areas. The fruit requires 40–55 days to mature, and the seeds presumably are dispersed by ants, which have been observed attacking the fleshy placentas.

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Tribe Pyroleae D. Don

15. **Chimaphila** Pursh, Fl. Am. Sept. 1: 279, 300. 1814.

Low, suffruticose to nearly herbaceous plants with long, scaly, creeping subterranean rhizomes and short, evergreen aerial shoots with alternate to subopposite or almost whorled, coriaceous, often shining, serrate, short-petioled leaves. Rhizomes with distant scale-leaves, each with an axillary bud and an associated root; roots reported to form adventitious buds. Inflorescence a stalked, terminal 1–8-flowered corymb, each flower in the axil of a deciduous [or persistent] bract, the pedicels lacking bracteoles. Flowers 5-merous, regular, fragrant, nodding. Sepals 5, united at the base, persistent. Petals 5, distinct, white to pink, concave, orbicular, forming a saucer-shaped corolla. Stamens 10; filaments enlarged and hairy at or below the middle; anthers extrorse in bud but at anthesis inverted by the inflexion of the apex of the filament, opening by a pore at the apparent apex (the base) of each of the divergent anther-halves (cf. *Arbutus*, *Arctostaphylos*); pollen in tetrads, 3-colpate. Stigma peltate, 5-lobed; style very short, top-shaped, immersed in the summit of the ovary; ovary superior, depressed-globose, 5-locular below, the placentae axile, but 1-locular above, the placentae becoming parietal (cf. *Epigaea*); ovules numerous, anatropous; disc circular, nectariferous, at the base of the ovary. Capsule depressed-globose, erect, 5-lobed, loculicidally 5-valved, the valves smooth on the edges; seeds small, numerous, with a thin cellular coat, an endosperm of a few large cells and a minute, undifferentiated embryo. Lectotype species: *C. maculata* (L.) Pursh; see Britton & Brown, Ill. Fl. North. U. S. ed. 2. 2: 672. 1913. (Name taken from the common name "wintergreen," from Greek, *cheima*, winter, and *philos*, friend.) — Wintergreen.

A well-marked boreal genus of about four or five species, including *Chimaphila umbellata* (L.) Bart., of circumboreal distribution with disjunct stations southward in Mexico and Guatemala and a close relative, *C. dominigensis* Blake, in Hispaniola; *C. japonica* Miq., in eastern Asia; *C. Menziesii* (R. Br.) Spreng. ($2n = 26$), from British Columbia to California, Sonora, and Jalisco; and *C. maculata* in eastern North America and Central America.

A number of geographical variants have been recognized in the widespread *C. umbellata*. The plant of eastern North America is var. *cisatlantica* Blake, which occurs from eastern Quebec to western Ontario, southward to Virginia, North Carolina, and Georgia, Ohio, Michigan, northeastern Illinois, and Minnesota; var. *umbellata* ($2n = 26$) is of Eurasian distribution. *Chimaphila maculata* ranges widely in dry woods, from southern New Hampshire westward to Michigan and northeastern Illinois, southward to Georgia, Alabama, and Tennessee, and, as a more robust form (apparently with larger flowers and fruits), from the mountains of Chihuahua and Sonora southward to Guatemala, Honduras, and Costa Rica.

The genus shares many features with *Pyrola*, from which it is readily distinguished by the corymbose inflorescence, enlarged staminal filaments, presence of a disc, and fruit with non-cobwebby valve margins.

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16. **Pyrola** Linnaeus, Sp. Pl. **1**: 396. 1753; Gen. Pl. ed. 5. 188. 1754.

Low, smooth, evergreen perennial herbs, with slender, creeping subterranean rhizomes (as in *Chimaphila*) and erect shoots bearing a cluster of petioled, coriaceous, persistent basal leaves and/or a raceme of [2]6–20 ascending, spreading or nodding flowers on an upright, more or less scaly-bracted scape; flowers in the axils of bracts, lacking bractlets on the pedicels. Flowers 5-merous, nodding, irregular [or regular]. Calyx 5-parted, persistent. Petals 5, concave, distinct, deciduous, [greenish-]white [to pink], imbricate in aestivation. Stamens 10; filaments glabrous, not enlarged, usually bent, the anthers then clustered on the upper side of the flower; anthers extrorse in the bud but in flower inverted by the inflexion of the apex of the filament, opening by a pore at the apparent apex (base) of each of the anther-halves, constricted [or not] below the pores, sometimes mucronate at the apparent base; pollen in tetrads, 3-colpate. Stigma of 5 narrow, erect lobes extending from the top of the style which forms a rim beneath the lobes; style [short to] long, [straight to] declined with the apex curved upward; ovary 5-locular below and the placentae axile,

but 1-locular above, the placentae becoming parietal; ovules numerous, anatropous; disc lacking. Capsule 5-lobed, loculicidally 5-valved, the valves cobwebby on the edges; seeds minute, as in *Chimaphila*. (Excluding *Ramischia* Opiz.) LECTOTYPE SPECIES: *P. rotundifolia* L.; see Britton & Brown, Ill. Fl. North. U. S. ed. 2. 2: 668. 1913. (Name Latin, diminutive of *Pyrus*, pear, from the somewhat similar leaves.)

A circumboreal genus, sometimes overestimated at 40 species, distributed southward along the higher mountains to Central America (Guatemala) and southeastern Asia (Sumatra). About six species occur in northeastern North America. The circumboreal *Pyrola rotundifolia* L. ($2n = 46$) reaches our area as var. *americana* (Sweet) Fern., distributed from Quebec to Ontario, southward to North Carolina, Tennessee, Kentucky, northern Indiana, Michigan, Wisconsin, and Minnesota. A report of *P. elliptica* Nutt. from Tennessee is unconfirmed, the species apparently not being known with certainty south of West Virginia.

The few chromosome numbers thus far determined support the separation of *Ramischia* Opiz (*Pyrola secunda* L., $2n = 38$) and of *Moneses* S. F. Gray (*M. uniflora* (L.) A. Gray, $2n = 26$), but not that of *Erxlebenia* Opiz (*P. minor* L., $2n = 46$), from *Pyrola* in which the diploid numbers are 46 or 92.

Both *Pyrola* and *Chimaphila* show tendencies toward vegetative reduction which culminate in the herbaceous *Moneses uniflora*, in which the rhizome has been eliminated, the aerial shoots arising from adventitious buds on the roots. The four genera of the tribe form a natural group which seems to have its closest affinities with Andromedeae and Arbuteae, although there can hardly be a direct relationship. Aside from the tendency toward reduction of the plant body and of the size and complexity of the seed and embryo, the group has no combination of features which distinguishes it from the Ericaceae proper.

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Subfam. MONOTROPOIDEAE Gray ('Monotropeae')

Tribe MONOTROPEAE D. Don

17. **Monotropsis** Schweinitz in Elliott, Sketch Bot. S. C. & Ga. 1: 478. 1817.

Low, smooth, reddish to purplish-brown (violet, pink, or white) plants with the aspect of *Monotropa Hypopithys*, lacking chlorophyll, the stem bent, emerging from the ground center part first, the plant hidden beneath fallen leaves, flowering in early spring. Rhizome lacking, erect flowering stems from adventitious buds from the roots, as in *Monotropa*. Stems with spirally arranged obovate, obtuse, scalelike bracts, the flowers 1–16 in a dense terminal raceme, each flower in the axil of a bract and the pedicel with 2 bracteoles. Flowers 5(4–8)-merous, nodding, very fragrant. Calyx of 5 oblong-lanceolate erect, distinct, persistent, scalelike sepals. Corolla campanulate, sympetalous, 5-lobed, slightly 5-gibbous at the base, the lobes ovate, 1/3–1/4 the length of the tube, persistent. Stamens 10; filaments filiform; anthers short, with a conspicuous connective, unappendaged, 4-locular at first but becoming 1-locular, horizontal at first but becoming inverted in flower (as in *Pyrola* and *Chimaphila*) and opening by 2 terminal pores in the apparent apex; pollen grains single, 2-colpate. Stigma large, capitate, not evidently lobed; style short, thick; ovary superior, 5(4)-locular at the base, each locule with a divided axile placenta, becoming 1-locular above, the placental halves then becoming parietal forming 5(4) conspicuous placentae; ovules anatropous, the integument of 2 layers of cells, embryo sac of the Polygonum type; disc 10-lobed, the lobes in pairs, each clasping the base of a petalad stamen. Fruit a subglobose berry remaining inclosed in the persistent corolla, filled by the enlarged placentae and the numerous minute, ovoid, unappendaged, red or orange seeds; seeds with an endosperm of a few cells and a globular (4-celled?) embryo. (*Schweinitzia* Nutt., *Cryptophila*

Wolf.) TYPE SPECIES: *M. odorata* Schwein. in Ell. (Name composed of *Monotropa* plus Greek, *opsis*, appearance, resembling *Monotropa*.) — SWEET PINE-SAP.

A distinctive genus of one or two species of the southeastern United States. *Monotropsis odorata* ranges at least from eastern Maryland and Virginia to central North Carolina, eastern Tennessee, northern Georgia, and northern Alabama. Since the plant flowers and fruits under a cover of leaves it is usually overlooked, and it is possible that its range is much wider, especially southeastward. The cycle of the plant above ground extends from the fall of one year, when the flowering shoots first appear beneath the fallen leaves, through anthesis early the following spring (March–April), to fruiting in July or early August. Baldwin has demonstrated the changing proportions of corolla tube/lobes from bud to anthesis and has effectively disposed of *M. Lehmaniae* Burnham as the immature fall phase of *M. odorata*. The status of *M. Reynoldsiae* Gray, described from scrub-oak thickets near St. Augustine, Florida, and known elsewhere only southward in the Indian River region, is dubious but unsettled. In *M. odorata* the colored corolla is as long as, shorter, or longer than, the oblong sepals, while the white corolla of *M. Reynoldsiae* is about twice as long as the ovate or ovate-lanceolate sepals. Wolfe, in his careful study of *M. odorata* in Alabama, found, however, a wide range in size (4–20 cm.) and color (reddish pink to brownish red, light lavender to darker shades, pink, white with pink vascular bundles, or pure white) of the plant and a wide variation of the length of the sepals (7–13 mm.). As in *Monotropa*, neither size nor color of plant or corolla can be regarded as diagnostic, and corolla/sepal ratio should be treated with the utmost suspicion.

Pollen is shed in bud on the inner surface of the corolla lobes, and pollination is by insects attracted by the strong, spicy fragrance at anthesis. Seed disperal apparently is by ants which attack the berry with its fleshy, sweetish placentae; the seeds are relatively plump and hard, well adapted to this habit, in contrast to the slender, tailed, wind-dispersed seeds of *Monotropa*. (Compare other baccate-fruited *vs.* dry-fruited Monotropoideae; *Epigaea*; *Gaultheria* and *Leucothoë*.)

Monotropsis is of particular interest for the 2-bracteolate pedicels, the well-developed calyx of five sepals, the sympetalous corolla, and the relatively unspecialized anthers. Its relationships are with *Monotropa*, *Pityopus* Small, *Monotropastrum* Andres, the two last of which also have baccate fruit. All four are more specialized than *Pterospora* Nutt., *Sarcodes* Torr., and *Allotropa* Gray, which constitute the tribe Pterosporeae. *Pterospora* is especially notable for the appendaged anthers which strongly suggest those of Arbuteae. Aside from the reductions and specializations to be expected in connection with the parasitic habit, there seems to be no basis for setting the Monotropoideae apart as a separate family, for the details of morphology, anatomy, and embryology fit excellently with those of other Ericaceae.

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18. **Monotropa** Linnaeus, Sp. Pl. 1: 387. 1753; Gen. Pl. ed. 5. 183. 1754.

Low, fleshy, tawny to reddish to translucent white herbs, lacking chlorophyll, blackening in drying. Main root thick, horizontal, with a surrounding mass of short, fleshy, intertwined secondary roots, each incased in a mycelial sheath; rhizomes lacking, the stems from adventitious (endogenous) buds from the roots. Flowering stems with scales or bracts, the tip nodding at first (erect in fruit), with 1–15 flowers in the axils of bracts, bractlets absent. Flowers 5-merous or the terminal 5-merous, the others 3- or 4-merous. Calyx(?) of 1–5 lanceolate, deciduous, bractlike scales. Corolla appearing campanulate, of 5(3 or 4) erect, scalelike, distinct petals

saccate at the base and tardily deciduous. Stamens 10 or 8; filaments subulate, the outer whorl (opposite petals) shorter than the inner; anthers short, kidney-shaped, becoming 1-locular at anthesis, opening transversely through 2 curving slits; pollen grains single, 2- or 3-colpate. Stigma funnel-shaped to discoid, obscurely lobed opposite the petals; style columnar, thick and fleshy; ovary superior, 10–8-lobed, 5- or 4-locular at the base and 1-locular above with 5 or 4 bilobed parietal placentae; ovules anatropous, very numerous; disc 10- or 8-lobed, the lobes in pairs clasping the bases of the petalad stamens. Capsule ovoid, 10–8-grooved, erect, loculicidally 5- or 4-valved, the very thick placentae covered with numerous minute, elongate, tailed seeds with a very loose coat, very few large endosperm cells and a 9–2-celled embryo. (*Hypopitys* Hill.) LECTOTYPE SPECIES: *M. uniflora* L.; see Britton & Brown, Ill. Fl. North. U. S. ed. 2. 2: 674. 1913. (Name Greek, *monos*, one, and *tropos*, turn, the summit of the stem nodding, bent to one side.) — INDIAN PIPE, PINE-SAP.

A small, but widely distributed, genus of parasitic herbs of the Northern Hemisphere, including two or more species, both occurring in our area.

Section HYPOPITYS Gray (*Hypopitys* of authors), with several-flowered racemes, the terminal one usually 5-merous, the others 3- or 4-merous, the sepals 3–5 (mostly as many as the petals), the anthers opening by a continuous line into two very unequal valves, and the style longer than the ovary, includes *M. Hypopithys* L. (*Hypopitys lanuginosa* (Michx.) Nutt., *H. americana* (DC.) Small), pine-sap, a woodland plant distributed from Newfoundland to British Columbia, southward to Iowa, Louisiana, and Florida in the East and to Arizona in the West, with a wide Eurasian range, as well. The species is quite variable in size of plant, color, pubescence, indentation of margins of bracts, and proportions of ovary and style, on the basis of which a number of species have been erected. Only a single species seems to be represented in North America, but a careful study of variation is needed. Diploid chromosome numbers of European material of *M. Hypopithys* and *M. Hypophegea* Wallr. (*M. Hypopithys* var. *glabra* Roth), which differ in pubescent *vs.* glabrous filaments, styles, and inner surface of the petals, have been reported as 48 and 16 respectively.

Section MONOTROPA (§ *Eumonotropa* Gray), differing in the 1-flowered shoots, the more reduced calyx of 1–4 scales, the transverse anthers opening by two short slits, and the short, thick style, includes only *M. uniflora* L. (*M. Brittonii* Small), Indian pipe. A frequent woodland plant of North America from Newfoundland and Quebec to British Columbia, southward to Oregon, Montana, Minnesota, Missouri, Oklahoma, Texas, and Florida, the species is disjunct southward in Central America in the mountains of central Mexico, Guatemala, and Columbia, and occurs in Japan, central China, and the Himalayas, as well. A number of variants in color, size, and other minor characters have been proposed, but only a single wide-ranging species seems to be involved.

Monotropa Hypopithys is segregated by some as *Hypopitys* Hill, on

the basis of the several flowers, the stem anatomy (a flattened cylinder *vs.* a ring of ten bundles), and the number of grooves on the pollen grains (*2 vs. 3*), but the plants are so similar in all other features that they are here maintained in a single genus.[9]

The wide range of habitats from which *Monotropa* has been recorded (moist woods to sand dunes to sphagnum bogs, but always in association with trees) and the tight mycorrhizal underground masses of the plant are more in keeping with a parasitic habit than with the saprophytic mode often assigned to it. In a recent study Björkman found that the same mycorrhizal fungus occurs in *M. Hypopithys* and adjacent trees; that the mycorrhizal masses of *Monotropa* are associated with the roots of trees (although there is no direct connection between *Monotropa* and tree); and, on the basis of trenching and radioactive tracer experiments, that it is probable that "*Monotropa* obtains its energy requirements from the trees via the mycorrhizal fungus common to them both."

There is still some question as to whether the "sepals" of *Monotropa* are bracts or sepals.

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Subfam. VACCINIOIDEAE Endlicher ('Vaccineae')

Tribe VACCINIEAE D. Don

19. **Vaccinium** Linnaeus, Sp. Pl. 1: 349. 1753; Gen. Pl. ed. 5. 1754.

Evergreen or deciduous, often stoloniferous shrubs [sometimes epiphytic], rarely trees. Leaves alternate, short-petioled, entire or serrate; winter buds small, ovoid, with 2 or several outer scales. Flowers solitary in the axils of bracts or leaves, the more or less well-defined inflorescences thus racemose; inflorescences from buds of the preceding season, rarely reduced to 1 or 2 flowers; pedicels usually with 2 bracteoles. Calyx adnate to the ovary, the lobes 4 or 5, rarely obsolete. Corolla white or greenish to red, cylindric, urceolate or campanulate, 4- or 5-lobed or sometimes 4-parted to the base. Stamens 8 or 10; anthers with or without spurs on the back, lacking white disintegration tissue in the connective, the halves narrowed upward into tubes, opening by a terminal pore, without awns; pollen tetrads without viscin strands. Stigma small, simple or somewhat capitate; style straight; ovary [partly to] completely inferior, 4- or 5- or falsely 10-locular (then usually 10-locular above, 5-locular below) by the development of ingrowths of the ovary wall which unite with the axile, more or less enlarged and pendulous placentae; ovules usually numerous on the surface of the placenta; disc conspicuous, on the surface of the ovary. Fruit a [5–]many-seeded berry crowned by the persistent calyx lobes; seeds usually small. (Including *Batodendron* Nutt., *Cyanococcus* (Gray) Rdyb., *Herpothamnus* Small, *Hugeria* Small, *Oxycoccus* Hill, *Polycodium* Raf., *Rhodococcus* (Rupr.) Avorin.) LECTOTYPE SPECIES: *V. Myrtillus* L.; see Britton & Brown, Ill. Fl. North. U. S. ed. 2. 2: 698. 1913. (*Vaccinium*, the classical name of *V. Myrtillus*.) — DEERBERRIES, BLUEBERRIES, and CRANBERRIES.

A polymorphic genus of perhaps 150 species, mostly of the Northern Hemisphere, from the mountains of the tropics northward to the Arctic Circle. The genus is composed of a number of more or less well-marked subgenera and sections, these often of restricted geographical distribution; but the classification is not yet well worked out and opinions as to the segregation of sections, subgenera, or genera vary. *Vaccinium* is treated conservatively here (cf. *Rhododendron*), for many reticulate relationships

are evident between the various subgenera. (Note also natural and artificial hybrids between sections and subgenera.) Seven subgenera occur in the United States, subg. VACCINIUM (subg. *Euvaccinium* Klotzsch), including sects. VACCINIUM (§ *Myrtillus* Koch) and VITIS-IDAEA (Moench) Koch, entirely to the north and west of our range.

Vaccinium is taxonomically difficult and much herbarium material is inadequate for study. Collectors should note accurately height of plant, glaucescence of various parts, corolla shape and color, fruit color, habitat, and presence of other species or individuals of varying size in the same or adjacent habitats.

Subgenus BATODENDRON (Nutt.) Klotzsch (*Batodendron* Nutt.), in which the flowers are in bracteate racemes, the corolla campanulate and 5-lobed, the stamens included, the anthers spurred on the back, the style exserted from the corolla, the pedicels jointed beneath the flower, the ovary incompletely 10-locular, and the berry black, leathery, and persistent, includes *Vaccinium cubense* Griseb. (and perhaps other species), of Cuba and Hispaniola, *V. arboreum* Marsh., of the southern United States, and *V. leucanthum* Cham. & Schlecht. and *V. stenophyllum* Steud., of Central America. *Vaccinium arboreum* (including var. *glaucescens* (Greene) Sarg.), farkleberry or sparkleberry, is an easily recognized shrub or small tree (to ca. 9 m.) with a wide range from Florida westward to Texas (Edwards Plateau) and northward to southeastern Virginia, Illinois, southern Missouri, and Oklahoma. The common southeastern form has lustrous, persistent leaves; in the western part of the range a glaucescent phase appears and leaf proportions, size of bracts, shape of flower, pubescence, and glandularity change to varying degrees. A careful study of variation is needed. Small observed that this species is tolerant of calcareous soil.

Subgenus POLYCODIUM (Raf.) Sleumer (*Polycodium* Raf., *Picrococcus* Nutt.), the deerberries, in which the corolla is campanulate and open in bud, the stamens exserted and spurred on the back, the pedicels not jointed, the flowers in leafy or bracted racemes, the ovary incompletely 10-locular, the fruit greenish to nearly black and insipid, is a well-marked group ranging from Florida to Maine, westward to central Canada and Texas, and in Mexico along the Sierra Madre Oriental from Puebla to Nuevo León. About 27 "species" have been described, but the number is undoubtedly far lower. The taxonomy of the group is chaotic and no practical treatment exists. All of the characters used are variable, including leaf size (note dimorphism between flowering and vegetative shoots), size of plant, pubescence, glaucescence, fruit color, and presence or absence of stipitate glands. The corolla is open in the young bud and continues to enlarge (as in *Halesia*), making size-comparisons difficult. Transplant and crossing experiments, population and cytological studies are an absolute necessity before the biology of this group can possibly be understood. The few chromosome counts ($2n = 24$) suggest that the polyploidy so characteristic of subg. CYANOCOCCUS may be lacking here.

Subgenus HERPOTHAMNUS (Small) Uphof (*Herpothamnus* Small), in-

cludes a single isolated species in our area, *V. crassifolium* Andr. (*H. crassifolium* (Andr.) Small), $2n = 24$, a creeping or tailing, narrow- and coriaceous-leaved evergreen with condensed 1–5-flowered axillary racemes, the flowers in the axils of small bracts, the pedicels with 2 bracteoles of almost the same size as the bracts, the ovary 5-locular, the stamens 10 with hairy filaments and unspurred anthers with short tubules, the berries black, sweet. The species is localized in moist, sandy habitats on the Coastal Plain from South Carolina to southeastern Virginia. Camp has called attention to the curious nodular enlargement of the roots and has suggested a relationship to a few montane South American pendent epiphytic species in which a similar development occurs, observing further that a species epiphytic at lower altitudes may become terrestrial at higher, with an even greater development of the root enlargements.

Subgenus CYANOCOCCUS (Gray) Klotzsch (*Cyanococcus* (Gray) Rydb.), the blueberries, with flowers in racemes or clusters from axillary buds, corollas urceolate to cylindric or ovoid-campanulate with 5 short lobes, anthers spurless, filaments pubescent, ovary incompletely 10-locular, and berries blue or black and often glaucous, includes about 24 species of eastern North America (about 16 in the Southeast), perhaps 10 of Japan and Korea, and probably *V. Selerianum* (Loesen.) Sleum., of Chiapas, Mexico. Extensive field studies and careful morphological comparisons, along with a series of cytological and hybridization studies, have revealed many of the underlying causes of the taxonomic difficulties encountered in this subgenus in eastern North America. (See especially Camp [1945] and Darrow & Camp [1945] for biology, discussion, keys to North American species and hybrids, chromosome numbers.)

In the United States the subgenus comprises about nine diploids ($2n = 24$), twelve tetraploids (including *V. corymbosum* L., a hybrid complex of varying combinations of about six tetraploids to the north of the glacial boundary), and three hexaploids (including *V. Ashei* Reade, a complex alloploid involving about five tetraploids). Interspecific hybridization (often extensive) occurs at the diploid, tetraploid, or hexaploid levels, the principal barriers being geographical and ecological isolation with no interspecific sterility between homoploids. Segregation within alloploid complexes adds further complications, for some of the derivatives may simulate the parental species. Autoploidy is postulated for six species which appear to be more robust tetraploid counterparts of diploids; three other tetraploids (*V. myrsinites* Lam., *V. marianum* Wats., *V. fuscatum* Ait.) and the hexaploid *V. Constablaei* Gray appear to be of alloploid origin. Pentaploid hybrids, but no triploids, have been found in the wild. Individual plants may be self-sterile, but others of the same species may be partly or largely self-fertile.

Vaccinium hirsutum Buckl. ($2n = 48$), of the mountains of eastern Tennessee and western North Carolina, is aberrant in the subgenus in the glandular pubescence of flowers and fruit. Camp has raised the intriguing possibility (based on some early hybrids made by Coville) that this species may have arisen as an alloploid between subg. CYANOCOCCUS

and subg. POLYCODIUM and has suggested that a pubescent-leaved, black-fruited *V. vacillans* Torr. and a pubescent-leaved, nonglaucous, gland-bearing form of subg. POLYCODIUM be used in attempting to resynthesize *V. hirsutum*.

Blueberries are a commercial fruit crop of ever-increasing importance, and a number of cultivars including both selections from the wild and a series of artificial hybrids (begun by Coville) have been named. The low, diploid *V. angustifolium* Ait. ($2n = 24$) is the most important commercial species in the Northeast, while commercial plantations of highbush types on the Coastal Plain, from eastern Massachusetts southward to Florida and Louisiana, are largely *V. australe* Small, southeastern highbush blueberry ($2n = 48$), or (especially to the south) *V. Ashei*, rabbit-eye blueberry. *Vaccinium corymbosum* is cultivated to a slight degree.

Subgenus OXYCOCCOIDES (Benth. & Hook.) Sleumer (*Hugeria* Small), shrubs in which the leaves are deciduous, the flowers solitary in the axils of leaves, nodding on slender pedicels, the corolla deeply 4-cleft and the lobes revolute, the anthers with very long terminal tubules and usually spurless, the filaments short, hairy, the ovary 4-locular, and the fruit red to black, insipid to acid and pleasant tasting, comprises only *Vaccinium japonicum* Miq. (including vars. *sinicum* (Nakai) Rehd., of China, *lasiostemon* Hayata, of Formosa, and *japonicum*, of Japan and Quelpaert Island) and *V. erythrocarpum* Michx., of the southern Appalachians. *Vaccinium erythrocarpum*, mountain cranberry, a shrub to 2 m., is a plant of cool montane habitats from eastern Tennessee, and western North Carolina, to western Virginia and eastern West Virginia. The fruit varies widely in taste from insipid to pleasantly acid, and in color from red to black (f. *nigrum* Allard). Although this subgenus and subg. OXYCOCCUS are similar in many floral details, the two are undoubtedly of quite independent derivation and are not closely related. The anthers are usually spurless, but Hooker figured a plant with short spurs, and in an occasional individual some (but not necessarily all) anthers of a flower may bear (one or) a pair of very short divergent spurs.

Subgenus OXYCOCCUS Drude (*Oxycoccus* Hill), the cranberries, is a well-marked group of about three trailing, small-leaved, evergreen bog species of the Northern Hemisphere with 4-merous flowers, the corolla parted nearly to the base, the lobes linear-oblong and revolute, the ovary 4-locular, the anthers with very short filaments and very long tubules; spurless on the back, the flowers articulated to slender 2-bracteolate pedicels, axillary or in short racemes, the berry bright red and acid. *Vaccinium macrocarpon* Ait. (*O. macrocarpus* (Ait.) Pers.), cranberry, a diploid ($2n = 24$), ranges from Minnesota to Newfoundland and southward on the Coastal Plain to Delaware, southeastern Virginia, and eastern North Carolina, and in the mountains to West Virginia, western Virginia, northeastern Tennessee, and western North Carolina.[10] A second diploid, *V.*

[10] There is also in the Gray Herbarium a small fruiting specimen of *Vaccinium macrocarpon*, labeled in Asa Gray's hand, "Little Rock, Arkansas, Dr. Hasse, 1886," which is presumably the basis for reports of this species from Arkansas.

microcarpum (Turcz.) Schmalhaus. ex Busch (*O. microcarpus* Turcz.) occupies a more northern and western area in North America (Alberta and British Columbia to Alaska) and ranges across Eurasia to Iceland. The tetraploid and relatively variable *V. Oxycoccos* L. (*O. quadripetalus* Gilib.) combines the characters of the diploids and has a virtually circumpolar distribution, overlapping in part that of both diploids. In eastern North America it extends southward in cold bogs in the mountains to Pocahontas County, West Virginia.[11] Isolated, sterile, hexaploid plants ($2n = 72$), distinguishable primarily by larger size, have been reported from Europe. Hagerup thought these to have resulted from the hybridization of *V. Oxycoccos* and *V. microcarpum*, while Camp has suggested instead a derivation directly from the tetraploid and has further postulated both the sporadic occurrence of similar hexaploids throughout the range of *V. Oxycoccos* and the possible occurrence of fertile hexaploids. *Vaccinium macrocarpon* is an important commercial plant, the crop of cranberries from Massachusetts, New Jersey, and Wisconsin (and to a lesser extent Oregon, Washington, Maine, and Rhode Island) amounting to 10–20 million dollars annually.

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Under family references see also BELL & BURCHILL, DUFRENOY, KEARNEY, MATTHEWS & KNOX, PELTRISOT, SMITH, and STANLEY; under *Gaylussacia* see CAIN & POTZGER; for special information on *Vaccinium macrocarpon* see Cranberries, the national cranberry magazine (Wareham, Massachusetts, 1936+).

[11] Fernald (Gray, Man. Bot. ed. 8. 1950) records *Vaccinium Oxycoccos* var. *ovalifolium* Michx. from North Carolina. Apparently this record is based on a sheet in the Gray Herbarium which bears two collections, both labeled in Gray's handwriting. To the left is a fruiting specimen of *V. Oxycoccos* with "N. Carolina, Croom" beneath it; to the right are two flowering shoots of *V. macrocarpon* and a characteristic blue label "Herb. Asa Gray" (on which the smaller label "Syn. Fl. N. Amer." has been pasted) with "Vaccinium macrocarpon. W. New York," also in Gray's hand. Another sheet bearing five collections of *V. Oxycoccos* has two small fruiting specimens which are associated with a similar label with "Vaccinium Oxycoccus. W. New York." Croom's botanizing seems to have been confined mostly to the Coastal Plain, especially around New Bern, North Carolina, and Tallahassee and Aspalaga, Florida, with observations obtained in the course of his travels between these areas. (See Jour. N. Y. Bot. Gard. 21: 164. 1920.) His published botanical notes do not list montane plants (with the exception of *Pinus pungens* which he recorded from Pilot Mountain, Stokes County, North Carolina), and I have been unable to find any evidence that he collected in the high mountains of western North Carolina where *V. Oxycoccos* might possibly be expected. Furthermore, he listed *Oxycoccus macrocarpus* in his *Catalogue of Plants Native or Naturalized in the Vicinity of New Bern, North Carolina* (1837). In view of these circumstances and of the two labels bearing "W. New York," it seems likely that an error in mounting or labeling is involved and that the specimen of *V. macrocarpon* should be attributed to Croom, while that of *V. Oxycoccos* should be assigned to New York. It is also significant that Gray himself (Syn. Fl. N. Am. 2(1): 26. 1886) did not admit *V. Oxycoccos* south of the mountains of Pennsylvania, whereas *V. macrocarpon* was given a range including Newfoundland and North Carolina. Until more convincing evidence is presented, it seems best to regard Pocahontas County, West Virginia, as the approximate southern limit of *V. Oxycoccos* and to exclude this species from the flora of the southeastern United States.

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20. **Gaylussacia** Humboldt, Bonpland & Kunth, Nova Gen. Sp. Pl. 3: ed. fol. 215, ed. quart. *275*. *pl. 257*. July 1819, nom. cons.[12]

Evergreen or deciduous, branching, often stoloniferous shrubs with the aspect of *Vaccinium*. Leaves alternate, short-petioled, entire or toothed, membranaceous to coriaceous, often with glandular hairs; winter buds ovoid with about 3 outer scales. Flowers in axillary, usually few-flowered and sometimes much condensed racemes from buds of the preceding growing season, bracteate, the bracts persistent to deciduous; pedicels with (1 or) 2 bractlets. Calyx adnate to the ovary, 5-lobed, persistent. Corolla white, greenish to red, ovoid or campanulate, 5-lobed. Stamens 10, inserted on the base of the corolla; filaments short; anthers unappendaged on the back, each half narrowed upward into more or less of a tube and opening by a terminal pore or short slit, awnless, without disintegration tissue; pollen tetrads without viscin strands. Stigma more or less capitate and 5-angled; style straight; ovary inferior, 10-locular, each locule with a single axile, campylotropous ovule; disc conspicuous, on the surface of the ovary. Fruit a berry-like drupe with 10 smooth, 1-seeded lenticular nutlets (pyrenes), crowned by the persistent calyx lobes, black or blue, sometimes glaucous. (Including *Buxella* Small, *Decachaena* Torr. & Gray, *Lasiococcus* Small.) TYPE SPECIES: *G. buxifolia* HBK. (Named in honor of Joseph Louis Gay-Lussac, 1778–1850, eminent French chemist and physicist.) — HUCKLEBERRIES.

A genus of perhaps 50 species of eastern North America and of South America, with the center of diversity in southeastern Brazil; lacking in Central America and the West Indies. Three well-marked sections including six to nine species occur in eastern North America; the application of subgeneric categories to the South American species is not yet well worked out.

Section GAYLUSSACIA (§ *Eulussacia* Benth. & Hook.), includes two species of our area with clavate-stipitate gland hairs in which the glandular portion is usually without a conspicuous secretion pellicle. *Gaylussacia Mosieri* Small (*Lasiococcus Mosieri* (Small) Small), with conspicuously glandular-hirsute hypanthia, is a plant mostly of sandy bogs from western

[12] Conservation superfluous. *Adnaria* [*odorata*] Raf., 1817, against which *Gaylussacia* was conserved, has been shown by Camp to be *Styrax* [*americanum* Lam.]. See Castanea **6**: 82. 1941 and Taxon **9**: 75. 1960.

Florida and southwestern Georgia to eastern Louisiana. The widespread *G. dumosa* (Andr.) Gray (*Lasiococcus* Small), with inconspicuous short-stalked glands on the hypanthium, ranges from southern Florida northward mostly on the Coastal Plain to Newfoundland, and westward to eastern Louisiana, with scattered stations inland across all but northwestern Alabama, in Coffee County, Tennessee, in the mountains of northern Georgia, North Carolina and Virginia and West Virginia, and in Pennsylvania. Southward a plant of drier soils, northward the species usually occurs in bogs. Considerable variation occurs in the length of the hairs on the hypanthium, those of some collections appearing to be almost intermediate in length with *G. Mosieri*; *G. orocola* (Small) Camp, described from a single collection from Flat Rock, Henderson County, North Carolina, may be one of these. The variation and interrelationships of these three taxa need further study.

Section DECAMERIUM (Nutt.) Benth. & Hook. (§ *Decachaena* (Torr. & Gray) Sleumer), including in our area plants with the leaves bearing capitate subsessile glands with a conspicuous golden secretion layer, and usually with the inflorescence bracts deciduous, is represented by *G. baccata* (Wangenh.) K. Koch ($2n = 24$), wide-ranging from Newfoundland to Manitoba, southward inland to Iowa, Kentucky, and northern Georgia, in which the leaves are golden-glandular on both leaf surfaces, and by three or four species in which the glands are confined to the lower leaf surface. *Gaylussacia ursina* (M. A. Curtis) Torr. & Gray ex Gray, with pubescent stamen-filaments, is a clear-cut forest species of the mountains of eastern Tennessee, western North Carolina and South Carolina, and northern Georgia. The relationship of *G. frondosa* (L.) Torr. & Gray ex Torr., a shrub to 2 m. high, confined mostly to the Coastal Plain from Florida to Louisiana and northward to southeastern New York, Massachusetts, and southern New Hampshire, to two similar stoloniferous shrubs, the very glaucous *G. nana* (Gray) Small (1–4 dm. high) and the very hairy and nonglaucous *G. tomentosa* (Gray) Small (to 1 m. high), both ranging from southern Georgia and Florida to southern Alabama, is uncertain. Camp tentatively maintained the two latter at the rank of species, suggesting that chromosomal counts might clarify the interrelationships (as in *Vaccinium* § *Cyanococcus*).

Section VITIS-IDAEA Benth. & Hook. includes only *Gaylussacia brachycera* (Michx.) Gray (*Buxella* Small), the box-huckleberry or juniperberry, a low, evergreen species completely lacking glandular hairs, which occurs in scattered localities on the coastal plain of Delaware and Maryland and on mostly north-facing slopes in Pennsylvania, southeastern West Virginia (the area of greatest abundance), eastern Kentucky, and eastern Tennessee. Most colonies seem to consist of single individuals (one in Pennsylvania some eight acres in extent estimated to be 1200 years old) which are largely self-sterile. (*Gaylussacia baccata* has also been observed to be self-sterile. The flowers in this species are homogamous and are cross-pollinated by *Apis* and various andrenid bees.)

Although Small considered the North American species to represent

three genera distinct from South American *Gaylussacia*, Camp has shown numerous interlocking relationships (e.g., the remarkable similarity of *G. Mosieri* and the Brazilian *G. pseudogaultheria* Cham. & Schlecht.). Camp concludes, in part, "Considered alone the North American material consists of three well-marked groups, but when critically examined each of these gives clear indication that it has been rather directly derived from South American material, having counterparts in the common plexus of the genus. . . . It is certainly clear that any separation into subgeneric categories on a geographic basis violates the fundamental phylogeny of the group."

On the basis of the 10-locular, 10-ovulate ovary and the fruit with 10 smooth, 1-seeded nutlets, *Gaylussacia* is sometimes segregated as a separate tribe, Gaylussacieae Small.

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STUDIES IN THE THEACEAE, XXX
THE AFRICAN SPECIES OF TERNSTROEMIA

Clarence E. Kobuski

The genus *Ternstroemia* is the largest genus of the family Theaceae with a nearly equal distribution of taxa in the tropical and subtropical regions of both the Eastern and Western Hemispheres.

In 1942 and 1943, three papers * dealing with the genus in the Western Hemisphere were published. The author was very much handicapped in that work since the study was made during the early war years and the European types of the genus were not available to him. The present study is a part of one encompassing the remaining members of the group, those of the Eastern Hemisphere. As in the treatment of the western species the results will be published in a series of papers based on regional distribution. There are several reasons for this manner of presentation. First, the taxa are generally quite endemic within a small area of distribution. The characters available for clear-cut distinction between taxa are very few and variable. Hence, a regional treatment is very helpful to any future worker, since he need consider only the taxa from a proscribed area. By the same token it is helpful to the author especially in making a key. To make a workable key to the complete genus may be possible — but hardly probable. An intense study of the group shows that there are many intangibles which the author learns to recognize but cannot use in presenting a key. This is especially true in the Indonesian species, which have been studied and will be treated later.

The genus *Ternstroemia* was first proposed by Linnaeus f. in 1781. Various other names have been applied to this genus, such as *Taonabo* Aublet (1775), *Dupinia* Scoparius (1777), *Hoferia* Scoparius (1777), *Tonabea* Jussieu (1789), *Amphania* Banks (1821), *Reinwardtia* Korthals (1840), *Llanosia* Blanco (1845), *Erythrochiton* Schlechter (1846), *Voelckeria* (1847) and *Mokofua* Kuntze (1891). *Taonabo* is the *nomen prius* of this group of synonyms and until a few years ago was used by several of the American botanists who followed the rule of strict priority laid down by the "American Code" of nomenclature. However, the name *Ternstroemia* has been included in the International Code of Botanical Nomenclature as one of the *nomina conservanda* and the name *Taonabo* listed as a *nomen rejiciendum*, thus ending any controversy which might have existed over the correct name.

The description below applies to the entire genus, the portions inapplicable to the African species being inclosed in brackets.

* Jour. Arnold Arb. **23**: 298–343, 464–478. 1942; **24**: 60–70. 1943.

Ternstroemia Mutis ex Linnaeus f. Suppl. Pl. 39. 1781.

Flowers hermaphroditic, dioecious [or androdioecious]. Sepals 5, imbricate, persistent. Petals 5, connate at the base [free or joined to the middle or above], stamens 15–∞, 2–several-seriate, rarely 1-seriate; filaments connate, the outer filaments adnate to the base of the corolla; anthers oblong or linear, as long as or longer than the filaments, dehiscing longitudinally, the connective usually projected into an apiculate or caudate appendage, rarely muticous. Ovary 2[3, rarely 1]-loculate, the ovules in each locule 2[–20], rarely solitary, pendulous from the apex of the placenta on more or less evolute funiculi. Style 1, entire [or rarely 2- or 3-parted], stigma or stigmata punctiform or evolute, entire or lobate. Fruit irregularly dehiscent, often explosively so. Seeds usually 4 [rarely 2–16]; testa opaque, smooth, rarely plicate-rugulose, yellow, usually covered with reddish, many-celled papilli; endosperm pulpy, ± developed, seldom lacking; embryo bent nearly double, oily, with half-terete or flat cotyledons.

Glabrous trees or shrubs with branches usually verticillate or subopposite. Leaves spirally disposed, congested or verticillate at the apex of the current year's growth, usually coriaceous, rarely chartaceous, entire or subentire. Flowers axillary, solitary, bracteolate, the bracteoles 2 [rarely 4], opposite or subopposite, placed immediately below the calyx, rarely with one somewhat removed and alternate on the pedicel.

TYPE SPECIES: *Ternstroemia meridionalis* Mutis ex Linn. f.

KEY TO SECTIONS AND SPECIES

Flowers hermaphroditic. Leaves thick-coriaceous. Stamens 15–20, arranged in a single series. Ovary semiglobose, 2-loculate, each locule 2-ovulate. Stigma 2-punctate. Angola. § TERNSTROEMIA. *T. africana.*
Flowers dioecious. Leaves chartaceous-coriaceous. Staminate flowers: Stamens many, ca. 60, arranged in several series. Pistillodium negligible or lacking. Pistillate flowers: Stamens much reduced in character, arranged in two series. Ovary 2-loculate, each locule 2-ovulate. Stigma bilobed, each lobe rounded and convex, ca. 2 mm. across. Tanganyika. . . . § ERYTHROCHITON. *T. polypetala.*

Ternstroemia africana Melchior, Notizbl. Bot. Gart. Berlin 8: 659. 1924; Nat. Pflanzenfam. ed. 2. 21: 142. 1925. — Exell, Jour. Bot. 74: Suppl. 21. 1936. — Exell & Mendonça, Consp. Fl. Angol. 1: 131. 1937.

Adinandrella congolensis Exell, Jour. Bot. **65**: Suppl. 30, *fig.* 1927. "*congolense.*"

Tree, glabrous throughout; branchlets generally terete, longitudinally striate in drying, reddish or reddish gray, the younger branchlets angled-striate in drying. Leaves coriaceous, obovate or obovate-elliptic, (4–)8–10 cm. long, (2–)4–5 cm. wide, obtuse or rounded at the apex, rarely somewhat emarginate, cuneate at the base, the margin lightly recurved, entire, occasionally slightly subserrate near the apex, the midrib canaliculate

above, elevated below, the veins ca. 7 pairs, inconspicuous on both surfaces; petiole 5–8 mm. long, canaliculate above, lightly and distinctly glandular-denticulate along the margin. Flowers hermaphroditic, solitary, axillary; pedicel 3–4.5 cm. long, somewhat thickened at the apex; bracteoles 2, subopposite, immediately below the calyx, oblong, ca. 4 mm. long, 1.6–1.8 mm. wide, obtuse; calyx-lobes 5, coriaceous, 7–7.5 mm. long, ca. 6 mm. wide, suborbicular, rounded at the apex (sometimes emarginate and mucronulate), unguiculate at the base, chartaceous at the margin; corolla-lobes 5, membranaceous, lanceolate-ovate, 8–8.5 mm. long, 3–3.5 mm. wide, lightly connate at the base; stamens 15–20, arranged in a single series, the filaments 1–2 mm. long, adnate to the base of the corolla, the anthers 3.5–4.5 mm. long, narrowly lanceolate, projected at the apex into a subulate connective 0.5–1 mm. long. Ovary semiglobose to ovoid, 4–5 mm. long, 2–4 mm. diameter, 2-loculate, each locule 2-ovulate; style ca. 4 mm. long; stigma punctate. Fruit not known.

Angola: Zaire, at sea level, near the river Congo, Sumba, Lower Congo, *J. Gossweiler 8592* (BM, type of *Adinandrella congolensis* and lectotype of *T. africana*), Dec. 2, 1921.

Ternstroemia africana was described by Melchior in 1924. Three years later, Exell, working with a duplicate of the type and not knowing of Melchior's earlier disposition of the Berlin specimen, proposed *Adinandrella* as a new genus. Later, in 1936, Exell agreed with Melchior's treatment of the specimens and designated his *Adinandrella* as a synonym of *T. africana*. I had an opportunity to study the type of *Adinandrella congolensis* while at the British Museum in the summer of 1960 and am very thankful for Exell's "first mistake," as he termed it, because up until then I had not known of either the existence of Exell's species or its relationship to Melchior's *T. africana*. The original specimen with which Melchior worked at Berlin has been destroyed, hence the specimen in the British Museum should become the type for *T. africana*, as well as *Adinandrella congolensis*.

An attempt to obtain additional material this past year from the herbarium at Luanda, Angola, has been unsuccessful, leading one to believe that the species has been collected only once. As a result, no dissections of the flowers of this species have been available to me. However, since the two descriptions of Melchior and Exell are so alike, and, as I believe, accurate, I do not feel the lack too greatly.

Exell refers to the stamens as arranged in triads but does not appear certain of this arrangement. Melchior makes no comment on this arrangement. They both may be right. Since the stamens are arranged in a single series and are adnate to the base of the corolla and since there are approximately fifteen stamens it just may be that there are three stamens to each corolla-lobe. However, Melchior, who has studied the group more extensively than Exell and is more accustomed to the multiple series of stamens usually found in the genus, would give little attention to such an arrangement, accepting it as a single series, as would I.

The main differences between the two African species are actually those between the two sections as found in the Asiatic species and the American species. This species from Angola, on the west coast of Africa, resembles the American species and belongs to the section TERNSTROEMIA, to which most of the American species belong. On the other hand, *T. polypetala*, from eastern Africa, belongs to the section ERYTHROCHITON and resembles the majority of the Asiatic species. However, this suggestive geographical arrangement is of no true significance since there are members of both sections in both hemispheres.

The environments of the two species are strikingly different. Although both are found at approximately 5° S. Lat., *T africana* grows at sea level along the river Congo, while *T. polypetala* was collected at an altitude of about 5400 feet in the mist forest of Tanganyika.

Ternstroemia polypetala Melchior, Notizbl. Bot. Gart. Berlin 11: 1095. 1934.

Tree 10–12 m. high; branchlets verticillate or subverticillate, terete, gray. Leaves verticillate, disposed at the apex of the branchlets, chartaceous-coriaceous, obovate, 5–10 cm. long, 2–4 cm. wide, dark red above, paler beneath, rounded or obtuse at the apex, cuneate at the base, the margin involute, sparingly glandular-denticulate, the midrib depressed on the upper surface, elevated below, the veins ca. 7 pairs, conspicuous below because of red color of veins against lighter background of leaf-blade; petiole up to 7 mm. long, appearing winged because of fine tapering decurrence of the leaf-blade. Flowers dioecious, axillary, solitary; pedicel ancipitous, 2–3 cm. long, thickening somewhat toward the apex; bracteoles 2, alternate below the calyx, lanceolate, ca. 4 mm. long, 2 mm. wide, ridged on the median of the dorsal surfaces, a single gland at the apex; calyx-lobes 5, rounded, unequal, the outer two lobes thicker, ca. 3 mm. long and 3.5 mm. wide, the inner lobes 3.5–4.0 mm. long, 4.5 mm. wide, the margin subscarious. Staminate flowers: corolla-lobes basically 5 (occasionally 2–5 additional smaller modified petals), obovate, ca. 10 mm. long, 6.5–7 mm. wide, rounded at the apex, connate at the base; stamens ca. 60, in several series, very unequal in length (3, 4, 5 and 6 mm. long), the longer ones, in the outer series, with filaments 1.5 mm. long, connate, and adnate to the base of the corolla, the anthers ca. 3 mm. long, the connective projecting into a mucro 1.5 mm. long, the inner, smaller stamens more abundant, proportionally smaller in filaments and anthers, the mucro about the same as the longer outer stamens; pistillodium lacking. Pistillate flowers (not seen) fide Melchior: Stamens much reduced, fewer in number, in two series; ovary conical ovoid, 2-loculate, each locule 2-ovulate, the apex contracted into a short, entire style; stigma 2-parted, each part convex and rounded, ca. 2 mm. across. Fruit (not seen) conical, ca. 1.5 cm. long, 0.8–1.0 cm. diameter, often crowned by the persistent style and stigma; seeds normally 4, two to each locule, occasionally less in number by abortion, ca. 9 mm. long and 5.5 mm. across, covered with a yellow, mealy aril.

Tanganyika: Morogoro District, northwest side of the Uluguru Mts., near Lupanga, mist forest at 1800 m. alt., *H. J. Schlieben 3152* (Y, lectotype), Dec. 22, 1932 (tree 10–12 m., flowers yellowish white).

The collector of the type states in his notes that both flowers and fruit were collected and Melchior in his original description fortunately described both, for the original specimen has been destroyed. However, Yale University has a duplicate specimen of *Schlieben 3152* which has been available to me for study. This duplicate, which now must become the lectotype, is woefully lacking in both flowering and fruiting material. Only a single, unattached staminate flower with a broken pedicel was found in a packet on the sheet. Since this flower was unattached, I ventured to use it in a dissection for my study and carefully re-pressed the material for future reference.

It is odd that Melchior in his original description designated the species as belonging to the section ADINANDRELLA, the same name used generically seven years previously for Exell's Angolan species. To my mind the species belongs to the Asiatic section ERYTHROCHITON as I do not find enough variation to warrant the creation of a new section. I am certain that Melchior, like myself, had never associated Exell's *Adinandrella* with *Ternstroemia* or he would have mentioned it in his treatment of the species. Melchior does not designate the section ADINANDRELLA as new, and, knowing his fastidious methods of presentation, I feel that it probably had been initiated in some previous publication. If so, I have never encountered it in my studies.

The name *T. polypetala* was selected by Melchior because of the many "petals" found in the flower. The single dissection made by the present author showed five basic petals, obovate in shape, rounded at the apex and measuring about 10 mm. in length and 6.5–7 mm. in width. These are typical petals for the genus in arrangement and size, especially when compared with the arrangement and size of the five calyx-lobes. There were also six other "pseudo-petals," much smaller, measuring only 6 mm. long and 3.5 mm. wide, arranged between the basic petals and the stamens and appearing at first as a second petal series — which they are not. In *Ternstroemia*, the five petals, like the calyx-lobes, always increase in size and change in texture from the smaller, thicker, outer ones to the larger, more membranaceous, inner one. In *T. polypetala*, this is true of the five basic petals, but the inner "pseudo-petals" are all very membranaceous, definitely involute, and in an arrangement inconsistent with that of the true petals. The "pseudo-petals" are bunched in three groups: (1) a single "pseudo-petal" is between two outer petals; (2) two are together, one in front of the other, but again between two outer petals; and (3) three are together, two in front of an outer petal and the third between that and the next outer petal.

Throughout the genus the stamens are always connate at the filament base, and in the outer series the filaments are adnate to the base of the corolla. In flowers in which there are more than a single series, the stamens in the outer series are usually larger. The inner "pseudo-petals" in

T. polypetala are a part of the outer series of stamens and, therefore, are likewise joined with the regular petals at the base. At the points where the inner "pseudo-petals" are found, the stamens are joined to them, rather than to the outer petals.

Thus the arrangement, size, shape and stamen attachment all indicate that the inner "pseudo-petals" are modified stamens. Regrettably, only a single staminate flower was available, and the only known pistillate flowers have been destroyed. I cannot but feel, however, that the interpretation of the "pseudo-petals" as modified stamens is correct and that pistillate flowers will also prove to have only five basic petals since the stamens have already been recorded as reduced to staminodia in these flowers. However, this is an assumption which cannot be verified until more material is available.

STUDIES IN THE GENUS COCCOLOBA, X. NEW SPECIES AND A SUMMARY OF DISTRIBUTION IN SOUTH AMERICA

RICHARD A. HOWARD

THE GREATEST NUMBER OF SPECIES of the genus *Coccoloba* occurs in South America. In the preceding paper of this series critical notes were presented on the 159 species reported to occur in South America. These 159 species, after critical study, were reduced to 77 either worthy of recognition or so incompletely known that they could not be referred elsewhere with confidence. The unnecessarily large number of species previously described can be attributed to several factors, including a tendency on the part of many botanists to identify or concern themselves only with local or regional floras, thereby omitting consideration of species from adjacent regions; the failure to understand the morphological variation found on single plants; and the failure to recognize the complete or partial unisexuality of the flowers in the genus. The species of *Coccoloba* are mainly recognized on the appearance of the leaves. The particular identifying characteristics often seem to defy description and none has been found which lends itself to tabulation or analysis, largely due to the paucity of collections and the lack of critical field studies. A full and ample collection of a single species for complete understanding of its morphology should include detailed notes on the habit of the plant and all its branches. Specimens should be collected to show the leaves and shoot systems of adventitious growth as well as normal growth. Functionally staminate and pistillate flowering branches are needed along with fruiting branches. Specimens should be taken from several trees within a population, where possible, to show the effects of the environment. Such ideal material is gathered only by the monographer and then usually only after bitter experience with a difficult group. Recently an experienced botanical traveler returned from a motor trip across the state of Goyaz in Brazil. He asked, "What is the attractive *Coccoloba* with wand-like branches and brilliantly colored leaves, so common everywhere?" The answer could only be, "It might be a new species," for no such habit data are available for any species of the genus in South America.

The following new species are not based on the ideal material suggested above, but, as is usually the case, on the specimens on hand. After a study of many hundreds of herbarium sheets of the genus from South America it is clear that no appropriate names exist for these plants.

As I have indicated in previous papers the number of reliable characteristics useful in identification and classification of the species of this genus are few. The flowers and their parts show little variation, beyond that ex-

pected, in anthesis. The perianth segments vary in size and shape with their position in the bud. The functional stamens are always shorter than the perianth segments but appear to mature at different times and therefore increase in length at different rates, until all are approximately equal in length when the flower is fully open. The sterile stamens may equal the mature fertile stamens in length or may all be rudimentary, or one or two may be long and the remainder short, or the reverse situation may occur. The sterile pistil from the staminate flower may be as large as the fertile pistil in a flower with abortive stamens or may be very small and rudimentary. Determining the fertility of a pistil in an herbarium specimen, however, is extremely difficult; such observations really should be made by the collector. The styles and stigmas in both functional and non-functional pistils vary in size and shape, particularly so in flowers clearly staminate in function.

A description containing the words, "perianth segments ovate-oblong, 1.5–2 mm. long, 0.5–1 mm. broad, functional stamens with filaments 1.5–2 mm. long, functional pistil 1.5 mm. long, styles 2 or 3, stigmas punctate, occasionally lobed, non-functional stamens and pistils rudimentary, 0.5–1 mm. long," would apply to nearly every species described. The following descriptions therefore are limited to the most reliable characteristics which can be used to define the specimens cited.

Coccoloba colombiana, sp. nov.

Arbor, 4–6 m., ramulis teretibus, adpresse tomentosis; ocreis subcoriaceis, 2 cm. longis, tomentosis, deciduis; petiolis 1.5–2 cm. longis, supra basim ocrearum gerentibus, tomentosis; laminis obovato-oblongis vel obovato-ellipticis, 10 × 6 vel 14 × 10 cm. longis latisque, supra glabris, subtus tomentosis vel strigosis in nerviis vel axillis, apice acutis, basi cuneatis asymmetricis, nerviis primariis 8–12, arcuatis; inflorescentibus 13–17 cm. longis, rhachibus striatis, puberulentis et tomentosis, bracteis ovatis, puberulentis, ca. 0.5 mm. longis, ocreolis translucentibus, ca. 1 mm. longis, floribus masculinis 3 vel 4 per nodulum, floribus femineis 1, raro 2 per nodulum; fructu ignoto.

Colombia. Without definite location, *Vageler s.n.* (B–holotype). ATLÁNTICO: Barranquilla, Cabica, *Bro. Elias 1082* (W), *1469* (W).

The specimen selected as the holotype was collected by H. Vageler on November 29, 1923, in Colombia. The specific location in German script is "Robles," a location which cannot be found in current atlases. The specimen had been studied by Burret, who applied two unpublished names to the specimen, one of them honoring Vageler. The collection *Elias 1082* in the Vienna herbarium was identified with the same unpublished name. *Elias 1469* was identified by Standley as "*Coccoloba leptostachya,*" which is neither similar nor apparently related.

Coccoloba colombiana is similar to *C. lehmannii* and *C. nitida*, differing from both in the density of the flowers on the inflorescence, the origin of

the petiole above the base of the ocrea, and the asymmetrical nature of the leaf base.

Coccoloba duckei, sp. nov.

Arbuscula subscandens ramulis teretibus, crispo-ferrugineo-tomentosis; ocreis membranaceis, 1.5–2 cm. longis, pubescentibus; petiolis supra basim ocrearum gerentibus, 3–5 mm. longis, pilosis; laminis ovato-oblongis, puberulentis vel glabratis, tenuiter coriaceis, 5 × 3.5 vel 10 × 5.5 cm. longis latisque, apice acutis vel subrotundatis, basi rotundatis vel subcordatis, nerviis primariis 8 vel 10; inflorescentibus racemosis, 10–14 cm. longis, rhachibus striatis puberulentis, bracteis ovato-oblongis, 2.5 mm. longis, nigris, puberulentis vel ad marginem ciliatis, ocreolis membranaceis, 2.5 mm. longis; floribus masculinis 3 vel 4 per nodulum; floribus femineis et fructu ignoto.

Brazil. AMAZONAS: Boa Vista, *Ducke 1358* (A–holotype, F, NY, US).

This species is named in honor of its collector, an explorer of the Amazon area, Adolpho Ducke. The species resembles *Coccoloba obovata,* from which it differs in having a densely flowered inflorescence, smaller leaves, and shorter petioles.

Coccoloba llewelynii, sp. nov.

Coccoloba bolivarana Williams, Trop. Woods **68:** 39. 1941. nomen nudum; Howard, Jour. Arnold Arb. **41:** 220. 1960.

Arbor 8 m., ramulis sericeo-tomentosis glabrescentibus; ocreis translucidis, 12 cm. longis, glabratis, deciduis; petiolis ad basim ocrearum gerentibus, 2–4 mm. longis, sericeo-tomentosis vel glabratis; laminis obovato-ellipticis vel oblanceolatis, 8 × 3 vel 12 × 6.5 cm. longis latisque, puberulentis, costa tomentosa glabrescente, apice acutis vel abrupte breve acuminatis, basi contracto-rotundatis vel truncato-subcordatis, nerviis primariis 6–8; inflorescentibus tenuibus 8–12 cm. longis, nodulis distinctibus, rhachibus sparse tomentosis vel glabratis, floribus masculinis 1 ad 3 per nodulum, floribus femineis singularibus, bracteis late ovatis, membranaceis, 1 mm. longis, ocreolis bifidis, erectis, membranaceis; fructu ovoideo, 6 mm. longo, 4 mm. diametro, lobis perianthii coronatis, 1 mm. longis; acheniis ferrugineis.

Venezuela. ANZOÁTEQUI: Taguatagua, *Pittier 14893* (US). BOLÍVAR: El Tigre, near Río Cuchivero, alt. 90 m., *Llewelyn Williams 13374,* June 18, 1940, (F-holotype, K). MONAGAS: Caicara, *Foster Smith 239* (US).

The collection by Williams has been referred to previously under the invalid name *Coccoloba bolivarana* (Howard *loc. cit.*). Williams described this plant as a tree of eight meters with many trunks. The Smith collection is described as a bush. The species is distinct among South American Coccolobas through the short petioled obovate-elliptic leaves and the inflorescence with distinctly separated flowering nodules. In appearance

the specimens are similar to *C. obovata* and *C. venosa*. *Coccoloba llewelynii* differs from *C. obovata* in the type of inflorescence and in the point of attachment of the leaves. It also differs from *C. venosa* in the inflorescence and the fruit. The species is named for its distinguished collector of plants in the American tropics, Llewelyn Williams.

Coccoloba orinocana, sp. nov.

Arbuscula vel arbor parva, 2–5 m.; ramis majoribus lacuniatis, hornotinis teretibus, dense ferrugineo-pubescentibus; ocreis 3 cm. longis, membranaceis, tomentosis vel pilosis, deciduis; petiolis leviter supra basim ocrearum gerentibus, 10–15 mm. longis, tomentosis; laminis oblongis, late ovatis vel oblongo-obovatis, 7 × 3.5 vel 12 × 8.5 cm. longis latisque, frequente bullatis, subtus tomentosis vel pilosis, supra pubescentis in costa nervisque, apice rotundatis vel obtusis, basi rotundis vel leviter cordatis, nerviis primariis 9–14, arcuatis; inflorescentibus 18–25 cm. longis, rhachibus puberulentis, nodulis confluentibus, floribus masculinis 3 per nodulum, floribus femineis singularibus, bracteis late ovatis, 0.5 mm. longis, puberulentis, ocreolis membranaceis, 1–2 mm. longis, puberulentis; fructu ovoideo, 4 mm. longo, 4 mm. diametro, lobis perianthii imbricatis, 1/4 vel subaequalibus hypanthium, acheniis nitidis, cinnamomeis.

Venezuela. BARINAS: Pedroza, *Bernardi 1955* (NY). BOLÍVAR: Río Pargueni, *Wurdack & Monachino 39759* (A–holotype, NY); Río Parguaza below Raudal Maraca, *Wurdack & Monachino 40994* (A, NY); Río Parguaza, Cerro Negro Parado below El Carmen, *Wurdack & Monachino 40973* (A, NY). GUÁRICO: El Sombrero, *Pittier 12367* (A, G, US)

This species is superficially similar to *Coccoloba caracasana* but differs in the softer leaves which are commonly bullate, the arcuate ascending nervation, and the fruiting perianth which is not lobed to the base.

Coccoloba portuguesana, sp. nov.

Arbor parva, ramulis teretibus, dense brunneis crisposo-tomentosis; ocreis membranaceis, 1–1.5 cm. longis, dense tomentosis, deciduis, petiolis supra basim ocrearum gerentibus, 5–12 mm. longis, tomentosis; laminis obovatis, 5.5 × 3 vel 16 × 11 cm. longis latisque, coriaceis, rugosis, inter nerviis bullatis, subtus puberulentis sed crisposo-tomentosis vel pilosis in costa axillisque, apice obtusis, subapiculatis, basim versus cuneatis, minute cordatis, nerviis primariis 8–11; inflorescentibus 6–30 cm. longis, rhachibus multo-striatis, puberulentis, bracteis ovatis, 1 mm. longis, puberulentis, ad marginem ciliatis; ocreolis translucidis, 1–2 mm. longis, puberulentis; floribus masculinis 3–5 per nodulum, floribus femineis 1–2 per nodulum; pedicellis fructiferis 0.75–1 mm. longis, fructu ovoideo, 3 mm. longo, 3 mm. diametro, hypanthio pauce manifesto, lobis perianthii basim versus distinctibus; acheniis cinnamomeis.

Colombia. Without specific location, *Goudot* "3 1 "(P). **Venezuela.** PORTUGUESA: Ospino, *Pittier 12024* (A-holotype, G, M, NY). ZAMORA: Sabaneta de Barinas, *Mell s.n.* (NY).

Lindau (Bot. Jahrb. 13: 222. 1890) cited the Goudot collection in a list of specimens seen as "*C. spec.*" The collecting locality is uncertain but the specimen, although smaller in size than the Pittier and Mell material, is clearly referable here.

Coccoloba portuguesana resembles *C. charitostachya, C. warmingii* and *C. latifolia* in one or several characteristics. It differs from *C. charitostachya* in the cuneate leaf base, longer inflorescence and the fruiting perianth which is divided to the base. The species is distinct from *C. warmingii* in the ridged inflorescence axis and the pubescence and is clearly distinct in fertile material from *C. latifolia* through the racemose inflorescence and the smaller leaves.

Coccoloba steinbachii, sp. nov.

Arbor, 6 m., ramulis striatis, glabris; ocreis 1.5–2 cm. longis membranaceis, glabris; petiolis 1.5–3.5 cm. longis, supra basim ocrearum gerentibus, ad basim glabris, ad laminas pilosis; laminis ovatis vel ovato-oblongis, (5 × 3.5) 8 × 5.5 vel 14 × 9.5 cm. longis latisque, tenuiter coriaceis, inter nerviis bullatis, costa supra puberulente, subtus nerviis primariis tomentosis vel pilosis, apice abrupte acutis, basi obtusis, truncatis vel leviter cordato-truncatis, nerviis primariis 10–14, arcuato-adscendentibus; inflorescentibus 32–44 cm. longis, rhachibus, bracteis et ocreolis puberulentis, bracteis ovatis, ca. 1 mm. longis, ocreolis membranaceis, 1–1.25 mm. longis, floribus masculinis (2–)7–13 per nodulum, floribus femineis 1–2 per nodulum; fructu ignoto.

Bolivia. Junction of the Río Beni and Río Madre de Dios, *Rusby 1380* (GH, K, NY); San Carlos, Mapiri, *Buchtien 1768* (NY); Santa Cruz, Sara, Buena Vista, *Steinbach 5617* (A–holotype, G, GH, NY), Río Palometillas, *Steinbach 6604* (A).

The type was collected in flower on April 25, 1921. *Coccoloba steinbachii*, named for its collector, is superficially similar to *C. tiliacea* of Argentina. Plants of *C. tiliacea* produce both peltate and nonpeltate leaves. Specimens of *C. steinbachii* may resemble the nonpeltate leaf types of *C. tiliacea* but differ in having more numerous veins, the leaf blades bullate between the veins, a longer inflorescence, and shorter pedicels.

Britton and Rusby (Bull. Torrey Club 27: 129. 1900) referred *Rusby 1380* to "*Uvifera illhaensis*" from which *C. steinbachii* differs in having much longer inflorescenses, longer petioles and more numerous veins to the leaves.

Coccoloba wurdackii, sp. nov.

Frutex adscendens, ramulis teretibus striatisque, dense ferrugineo-puberulentis; ocreis 5 mm. longis, rigidis, persistentibus, subampliatis; petiolis ad basim ocreis gerentibus, robustis 5–8 mm. longis, puberulentis; laminis late ovatis vel ovato-oblongis, 9 × 4 vel 12 × 9 cm. longis

latisque, crasse coriaceis, glabris vel rare puberulentis, in sicco dense reticulatis, costa curvata, apice late acutis, basi cordatis vel rotundis, nerviis primariis 5 vel 8; inflorescentibus 10–15 cm. longis, rhachibus, bracteis, ocreolis dense puberulentis; floribus masculinis 2–5 per nodulum, floribus femineis singularibus, bracteis late ovatis, ca. 0.5 mm. longis, 1 mm. latis, ocreolis subampliatis, bifidis, ca. 1.0 mm. longis; fructu immaturo, ovoideo basi rotundato, lobis perianthii brevibus, coronatis.

Colombia. VAUPÉS: Río Guainia opposite Maroa, *Maguire, Wurdack & Keith 41852* (A holotype, NY). **Venezuela.** AMAZONAS: Maroa, *Maguire, Wurdack & Bunting 36443* (NY), *Maguire & Wurdack 35693* (A, NY).

This species is named in honor of Dr. John Wurdack, who along with Dr. Bassett Maguire, has contributed greatly to our botanical knowledge of northern South America. *Coccoloba wurdackii* is similar to both *C. schomburgkii and C. marginata*. It differs from the former in its liana habit, longer inflorescences, and larger, reticulately veined leaves. From *C. marginata* the species may be distinguished by its shorter, broader, and thicker ovate leaves and heavier inflorescence axis.

Coccoloba zuliana, sp. nov.

Ramuli teretibus; ocreis deciduis; petiolis ad basim ocrearum gerentibus, 2–3 mm. longis, glabris, laminis obovatis, 2.5 × 1.5 vel 5.5 × 2.5 mm. longis latisque, membranaceis, apice acutis, basi cuneatis, subtus in axillis sparse tomentosis, nerviis primariis 5–8; inflorescentiis 3–4 cm. longis, rhachibus striatis, bracteis ovatis, ad marginem ciliatis, ocreolis membranaceis, ca. 1 mm. longis; floribus ignotis; pedicellis fructiferis singularibus, erectis, adscendentibus, 2 mm. longis, fructu ovoideo, 4 mm. longo, 3 mm. diametro, hypanthio non-manifesto, lobis perianthii ad basim distinctibus, imbricatis, adpressis; acheniis triangularibus, ferrugineis.

Venezuela. ZULIA: Perija, *Tejera 140* (US–holotype, GH).

This species is known from a single collection but is clearly distinct from the other species of *Coccoloba* in Venezuela and in South America. The small leaves and short inflorescences with well developed peduncles mark this species. The peduncles, while only 2 mm. long, appear even longer in contrast to the thin rachis. No collector's data are available regarding the size or habit of the plant. The specimens have also lost all the ocreae. Clusters of hairs occur in the axils of the veins on the lower leaf surface. The remainder of the leaf surface, the remnants of the ocreae, and the inflorescence rachis show resinous dots which may represent hair bases or excretions of some form. *Coccoloba zuliana* appears to be related to *C. obtusifolia*, differing in the shape of the leaves, the straight peduncles and the ovate fruit. In leaf shape *C. zuliana* resembles some collections of *C. peruviana* but differs in the size of the leaves, as well as the length of the peduncles.

The distribution of the species of Coccoloba in South America. Numerals on the map refer to the number of species recognized in each state of Brazil and in the other countries of South America. No species have been reported from Chile. The dotted line indicates the recorded limit of distribution in northern Argentina.

DISTRIBUTION WITHIN SOUTH AMERICA

Nearly half of the species of *Coccoloba* reported from South America are inadequately known. The flowers of one sex or the other, the fruits, or the leaves from adventitious shoots may be needed for a complete understanding of the individual taxa. All attempts to produce a key to the species of the genus occurring in South America have been unsatisfactory. For the present, therefore, it appears most useful to list the species occurring in defined political and geographical areas. The largest number of species (44) occurs in Brazil, with 20 species reported from the state of Rio de Janeiro. Venezuela has 27 species. The largest number of inadequately known species also occurs in these two areas, especially the vicinities of Rio de Janeiro and Caracas. Many species from the neighborhoods of these two major cities are known only from the type collections made one hundred to two hundred years ago. Modern collectors have not located additional material. Whether the species or the habitats have been eliminated by the growth of these urban centers, or whether representatives of these species would be located by careful scrutiny of the remaining vegetation, only time will tell.

Collections representing the following species have been cited in this or the preceding paper of this series, or have been received recently from South American botanists. For ease in locating specific names the generic abbreviation has been omitted throughout.

Argentina

argentinensis, cordata, paraguariensis, tiliacea

Bolivia

cujabensis, longipes, meissneriana, mollis, persicaria, peruviana, spinescens, steinbachii, tiliacea

Brazil

ACRE: *acuminata, confusa, densifrons, duckei, lepidota, marginata, mollis, ovata, parimensis, peruviana, schomburgkii, spruceana*

ALAGOAS: *alagoensis*

AMAZONAS: *acuminata, confusa, densifrons, duckei, marginata, mollis, ovata, parimensis, peruviana, schomburgkii, spruceana*

BAHIA: *alnifolia, alagoensis, arborescens, cordata, cruegeri, ilheensis, laevis, marginata, mollis, ochreolata, ovata, pipericarpa, plantaginea, ramosissima, rosea*

CEARÁ: *latifolia, mollis*

ESPIRITO SANTO: *ochreolata*

GOYAZ: *densifrons, latifolia, marginata, mollis*

MARANHÃO: *latifolia, mollis, sparsifolia*

MATO GROSSO: *brasiliensis, cujabensis, longipes, mollis, peruviana*

MINAS GERAES: *acrostichoides, alagoensis, brasiliensis, cerifera, declinata, glaziovii, grandiflora, lanceolata, marginata, mollis, pipericarpa, sticticaulis, warmingii*

PARÁ: *acuminata, confusa, densifrons, ovata, parimensis*

PARANÁ: *glaziovii*

PERNAMBUCO: *alnifolia, laevis, mollis*

PIAUHY: *mollis*

RIO DE JANEIRO: *acrostichoides, alagoensis, alnifolia, arborescens, confusa, fastigiata, gardneri, glaziovii, grandiflora, laevis, mollis, ochreolata, peltata, pipericarpa, ramosissima, rigida, salicifolia, schwackeana, sticticaulis, warmingii*

RIO GRANDE: *cordata*

SANTA CATARINA: *arborescens, warmingii*

SÃO PAULO: *confusa, cordata, glaziovii, mosenii, warmingii*

British Guiana

acuminata, charitostachya, cruegeri, excelsa, gymnorrhachis, latifolia, lucidula marginata, ovata, parimensis, savannarum, schomburgkii, sparsifolia, striata

Colombia

acuminata, caracasana, colombiana, coronata, densifrons, dugandiana, filipes, lehmannii, nitida, obovata, obtusifolia, ovata, padiformis, portuguesana, trianaei, uvifera, venosa, wurdackii

Dutch Guiana

conduplicata, excelsa, gymnorrhachis, latifolia, marginata, mollis, uvifera

Ecuador

acuminata, coronata, densifrons, mollis, obovata, ruiziana

French Guiana

excelsa, latifolia, lucidula, marginata, mollis, parimensis

Paraguay

cordata, cujabensis, guaranitica, paraguariensis, spinescens

Peru

acuminata, coronata, densifrons, gracilis, mollis, nutans, padiformis, parimensis, peruviana, ruiziana

Uruguay

argentinensis, cujabensis

Venezuela

acuminata, caracasana, coronata, cruegeri, dugandiana, fagifolia, fallax, latifolia, laurifolia, lehmannii, lucidula, llewelynii, marginata, obtusifolia, orinocana, ovata, padiformis, parimensis, portuguesana, schomburgkii, spruceana, striata, swartzii, uvifera, venosa, wurdackii, zuliana.

THE GENERA OF THE CYRILLACEAE AND CLETHRACEAE OF THE SOUTHEASTERN UNITED STATES[1]

JOAB L. THOMAS

CYRILLACEAE Lindley (CYRILLA FAMILY)

Deciduous or evergreen shrubs or small trees, leaves simple, alternate, entire, exstipulate, short-petioled [sessile], glabrous. Inflorescences terminal or axillary racemes, each flower in the axil of an obovate, spatulate, or lanceolate, caducous or persistent bract; pedicels with [or without] 2 lanceolate or oblanceolate bracteoles. Sepals 5, rarely 6 or 7, equal [unequal], [quincuncially] imbricate in bud, ovate, lanceolate, or deltoid, persistent. Petals as many as the sepals, spatulate to oblong-elliptic, white or pinkish white [deep pink or violet]. Stamens 5–10, the insertion hypogynous, filaments terete or flattened and petaloid below the middle; anthers versatile, dehiscing through longitudinal slits [or morphologically basal pores]; pollen grains single, tricolporate (or tetracolporate), with wide longitudinal furrows which narrow in polar view to produce a Y-shape. Gynoecium syncarpous, ovary superior, 3–5-locular, each locule containing 1–3 ovules; style short, stigma 2–5-lobed [or not lobed]. Fruit indehiscent, globose or distinctly 3–5-winged, often devoid of seeds. Seeds without seed coats; endosperm cellular; embryo straight, cylindrical.

A small family of three genera and fourteen species, distributed along the Coastal Plain of the southeastern United States, in the West Indies, Central America, and northern South America. *Cyrilla* and *Cliftonia*, each containing but a single species, occur in our area. The third, *Purdiaea* Planch., is composed of 12 species, distributed in Cuba, British Honduras, Guatemala, and northern South America.

Most authors who have attempted a phylogenetic classification of the Cyrillaceae have placed this family either near the Celastrales or the Ericales, with a few suggesting a relationship with both of these groups. The Cyrillaceae have been shifted from one to the other many times, and

[1] Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium made possible through the support of George R. Cooley and the National Science Foundation, and under the direction of R. C. Rollins and C. E. Wood, Jr. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. 39: 296–340. 1958). Other published portions of these studies will be found in Jour. Arnold Arb. 40, 41. (See also the Ericaceae in this issue.) The area covered in this, as in former treatments, is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. Material included in descriptions which is inapplicable to species of this area is placed in brackets. References which have not been checked are marked by an asterisk. The figures of *Cyrilla* and *Clethra* were drawn by Dorothy H. Marsh, in part from material collected by R. B. Channell and H. F. L. Rock.

have been treated as a subfamily of both the Celastraceae and the Ericaceae. They were also occasionally changed from one of these groups to the other in later editions by the same author (Endlicher, 1840, 1841; Lindley, 1835, 1847). As the family has been studied in greater detail, however, the evidence has become increasingly strong for a close relationship between the Cyrillaceae and members of the Ericales, particularly the Clethraceae.

The Cyrillaceae have a well-documented fossil record, with cyrillaceous pollen grains occurring as far back as the Upper Cretaceous, thus indicating that the family is a relatively old one. Although these pollen grains cannot be definitely assigned to any of the living members of the Cyrillaceae, they are quite similar to the pollen of *Cyrilla* and *Cliftonia*. The best documented fossil record is in the Brandon Lignite of Vermont. The most abundant wood and the second most abundant pollen in this fossil flora is that of *Cyrilla* (Spackman, Traverse). The wood, and particularly the pollen, from this deposit is very similar to that of living material — remarkably so in view of the age of the deposit, estimated as late Upper Oligocene by Barghoorn.

The Cyrillaceae are distinguished from related families by the outer whorl of stamens opposite the sepals, the dry, indehiscent fruit, the ovary with 1–3 ovules per locule, and seeds without seed coats.

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KEY TO THE GENERA OF CYRILLACEAE

Stamens 5, filaments terete; fruit globose or subglobose, longitudinally bisulcate or trisulcate. ..... 1. *Cyrilla*.
Stamens 10, filaments broad and petaloid below the middle; fruit distinctly 3–5-winged. ..... 2. *Cliftonia*.

1. **Cyrilla** Garden ex Linnaeus, Mantissa Pl. 5. 1767.

Shrubs or small trees [up to 25 m. tall], usually branching near the base; bark light gray or brown. Roots shallow, usually running horizontally a few inches beneath the surface of the soil. Leaves simple, alternate, entire, exstipulate, short-petioled, subcoriaceous to coriaceous, dark green, shining above, pale beneath, often clustered toward the ends of branches, densely reticulate, the midvein prominent beneath, prominent or depressed above. Flowers in slender, glabrous, erect or pendulous racemes, borne near the ends of branches, in the axils of leaves or leaf scars of the previous growing season; pedicels articulate at the point of attachment to the rachis, persistent; bracts lanceolate, persistent; 2 bracteoles borne above the middle of the pedicel, alternate or opposite, lanceolate, persistent. Sepals 5, rarely 6, free or occasionally coalescent laterally at the extreme base, persistent, ovate-lanceolate to deltoid, imbricate in bud. Petals as many as the sepals, white or pinkish, inserted on a small glandular disc, membranaceous laterally and above the middle, thickened and glandular on the inner surface medially and below the middle. Stamens 5, opposite the sepals; filaments terete, subulate; anthers versatile, attached near the middle on the dorsal side, 2-lobed, the lobes free below the point of attachment to the filament, united above. Ovary sessile, 2- or 3(rarely 4)-locular, ovules pendulous, anatropous, 1–3 in each locule; stigma 2–4-lobed, the lobes equal to the number of locules. Fruit globose to ovoid or obpyriform, dry, indehiscent, often devoid of seeds, not more than 1 seed developing in each locule. Seeds pendulous, elongate; embryo elongate, cylindrical, the cotyledons short, inferior, the radicle superior. TYPE SPECIES: *C. racemiflora* L. (Named in honor of Dominico Cirillo, an Italian physician and professor at Naples.) — LEATHERWOOD, TITI.

A genus of a single species, *Cyrilla racemiflora* L., easily distinguished from other Cyrillaceae by the pair of persistent bracteoles on the pedicel, petals medially thickened and glandular, five stamens opposite the sepals, and three ovules per locule. It is a plant of acid, and usually sandy, soil along the margins of swamps and small streams and in wet pinelands, distributed in our area along the Coastal Plain from Florida to southeastern Virginia and to southeastern Texas. It also occurs in Mexico, British Honduras, the West Indies, and northern South America.

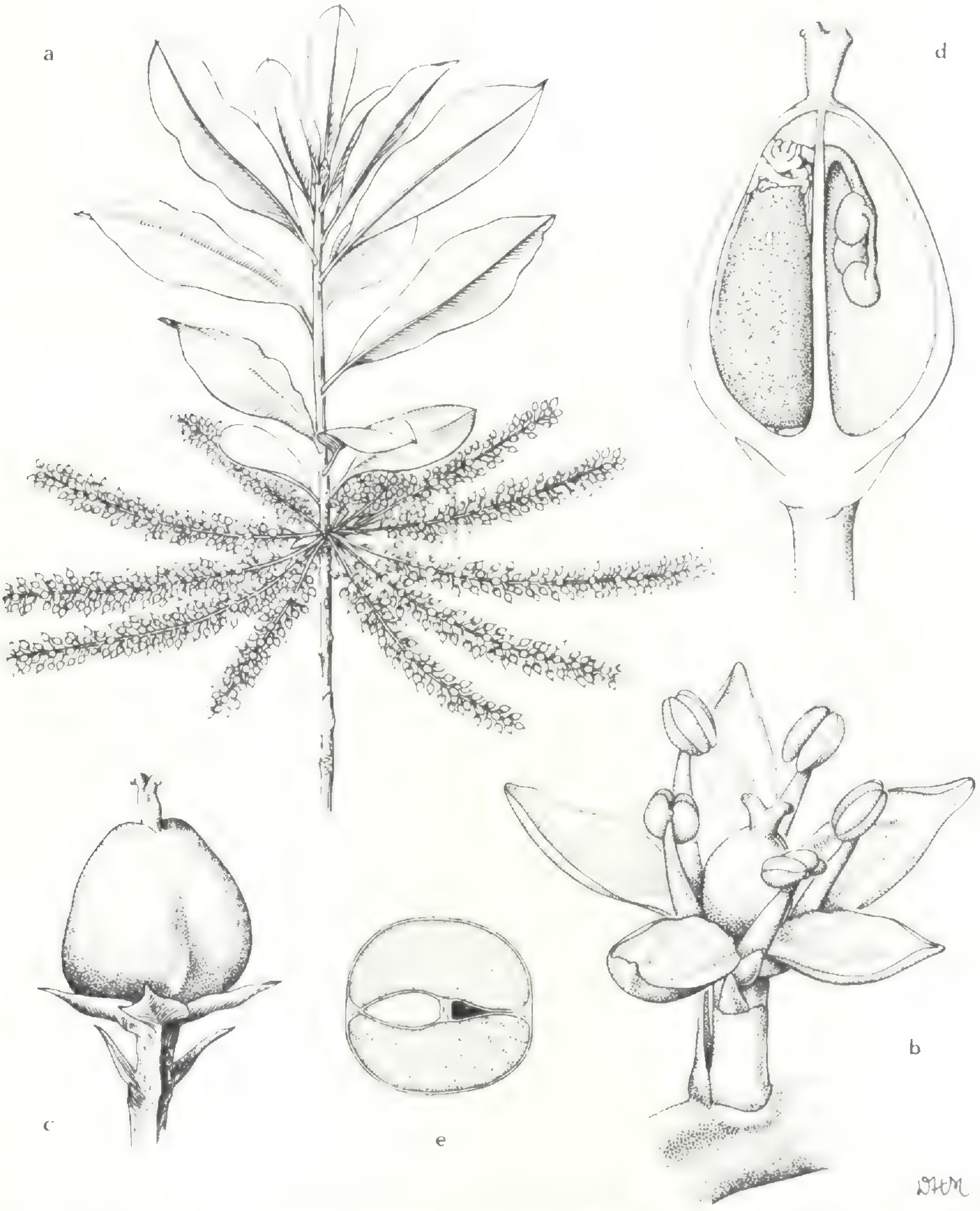

FIG. 1. **Cyrilla.** *C. racemiflora*: a, fruiting branchlet, × ½; b, flower, × 15; c, fruit, × 10; d, nearly mature fruit in vertical section — note large seed (not sectioned) filling left locule, three ovules in right locule, × 15; e, fruit, semi-diagrammatic cross section, position of seed in left locule shown by stippled area, embryo omitted — note parenchymatous development of pericarp, × 10.

This widespread species shows a high degree of local variation in the mountains of northern South America, in Oriente Province, Cuba, and in the southeastern United States, especially in northern Florida. On the basis of this variation, some authors have divided the group into several species, including *C. parvifolia* Raf. and *C. arida* Small in the Southeast. The different variation patterns are graded, however, with intermediate forms connecting the various extremes.

Cyrilla reproduces prolifically by means of adventitious shoots which arise from the roots. These root sprouts spread out radially from an individual, and as they increase in size and become established, they, in turn, give rise to additional sprouts. In some areas, clones of this sort become quite extensive and may cover an acre or more. The buds which give rise to the shoots are exogenous in origin, developing in or near the cork cambium, and apparently do not develop before the initiation of secondary activity. The buds remain in the root for three to four years before emerging as a shoot. During this time the bud establishes vascular connection with the root and increases in size at a rate which is just sufficient to keep pace with the secondary activity of the root.

This sprouting mechanism is the primary means of reproduction in the Cyrillaceae, for the abundant fruits produced each year rarely contain seeds. Parthenocarpic fruits of this type are found, almost without exception, toward the middle of a large clone, thus indicating that *Cyrilla* must have a rather high degree of self-sterility. Apparently self-fertilization provides sufficient stimulus to initiate fruit development, but seeds are developed only when a plant receives pollen from a different individual.

Cyrilla is occasionally cultivated as an ornamental in the southeastern United States and in a few botanical gardens outside that area on the East Coast and in Europe. It is valued for its graceful racemes of white flowers which bloom over a period of a month or more and are followed by small yellow fruits which are also attractive and persist until late autumn. In some areas *Cyrilla* is an important source of nectar for honey known locally as "titi" honey, in reference to one of the colloquial names for *Cyrilla*, and said to have a delicate and very delicious flavor.

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2. **Cliftonia** Banks ex Gaertner f. Fruct. et Sem. Pl. 3: 246. 1805.

Evergreen shrubs or small trees, usually branching near the base, rarely becoming up to 12 m. tall; bark reddish brown or gray, thick and spongy on the trunks of older trees; young stems dark red, smooth, becoming gray and scaly after 1–2 years. Leaves simple, alternate, entire, exstipulate, short-petioled, subcoriaceous or coriaceous; light green, shining above, pale, glaucous beneath; oblanceolate-elliptic or rarely obovate-oblanceolate, apex acute or slightly emarginate. Flowers in terminal or axillary racemes, glabrous; rachis attenuate, ridged, each ridge terminating in a small, concave mound at the base of a bract; bracts white or occasionally pinkish, usually turning brown above the middle, membranaceous, obovate-spatulate or spatulate, slightly concave and thickened basally, articulate at the base, caducous well before anthesis; 2 bracteoles borne alternately on the pedicel, usually shedding shortly after anthesis. Sepals 5, rarely 6 or 7, white or pinkish, deltoid, persistent, membranaceous at anthesis, becoming foliaceous at maturity. Petals white or pinkish, imbricate in bud, occasionally weakly clawed near the base, longitudinally 3-veined. Stamens 10 in 2 whorls of 5, the outer opposite the sepals and inserted lower on the receptacle than the inner which is opposite the petals; filaments laterally expanded and petaloid below the middle, narrowing abruptly, becoming terete and subulate above; anthers versatile, attached slightly below the middle. Ovary borne on a small, slightly concave, glandular nectariferous disc, 3–5-locular, each locule with a single, pendulous ovule; stigma massive, subsessile, 2–5-lobed. Fruit 2–5-winged, dry, indehiscent, usually devoid of seed, but sometimes with as many as 5. Seeds consisting of an elongate embryo with short cotyledons, surrounded by a mass of cellular endosperm. TYPE SPECIES: *Cliftonia monophylla* (Lam.) Britton ex Sarg. (Named in honor of D. G. Clifton, Chief Justice of West Florida) — BUCKWHEAT TREES.

A genus of a single species, *Cliftonia monophylla,* distributed along the Coastal Plain of southern Georgia, Alabama, Mississippi, and northern Florida. *Cliftonia* apparently has a very narrow ecological tolerance, as well as geographical range, occurring only in very wet, sandy, acid soils. It is nearly always found growing in association with *Sarracenia* L.

Cliftonia is very distinctive and is easily distinguished from related genera by the winged fruit which resembles that of *Fagopyrum,* the massive, 3–5-lobed, subsessile stigma, and the filaments which are laterally expanded and petaloid below the middle. In spite of its distinctiveness, *Cliftonia* was originally described as a species of *Ptelea* by Lamarck, apparently on the basis of the winged fruits.

The fruits of *Cliftonia,* as of *Cyrilla,* are usually parthenocarpic, and the plants reproduce primarily by root sprouts. In contrast to *Cyrilla,* however, *Cliftonia* shows very little variation throughout its range and has been treated as a monotypic genus by every author who has dealt with this group. The narrow geographic range and the lack of variation indicate that *Cliftonia* is probably a relict form in the present-day flora.

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CLETHRACEAE Klotzsch (WHITE ALDER FAMILY)

Deciduous shrubs or small trees with alternate, simple, exstipulate, serrate-margined leaves. Flowers in terminal racemes or panicles, bisexual, regular, the insertion hypogynous. Rachis, bracts and pedicels densely clothed with stellate [simple] trichomes. Sepals 5, persistent, quincuncially imbricate, united at the extreme base, free above. Petals 5, free, alternate with the sepals, deciduous. Stamens 10 [rarely 12], in 2 whorls of 5, the outer whorl opposite the petals, the inner opposite the sepals; filaments glabrous or pubescent, adnate to the corolla at the extreme base; anthers extrorse in bud, becoming inverted and introrse at anthesis by a straightening of the filament, dehiscing by means of apical (morphologically basal) slitlike pores; pollen grains single, tricolporate. Gynoecium syncarpous, the ovary superior, 3-locular, with axile placentation; ovules numerous, small, anatropous; style single, dividing near its apex into a 3-lobed stigma. Fruit a 3-valved, loculicidal capsule. Seeds numerous, small [occasionally winged], with fleshy endosperm and very thin seed coats, the embryo cylindrical. TYPE GENUS: *Clethra* L.

A small family composed of a single genus, *Clethra*, with 30–40 species primarily of tropical or subtropical Asiatic and American distribution. *Schizocardia* Smith & Standley, from Central America, was described in the Clethraceae, but is now known to be a species of *Purdiaea* (Cyrillaceae).

The Clethraceae were first raised to family status by Klotzsch on the basis of the regular flowers with separate petals, anthers with poricidal dehiscence, three-lobed stigma, and loculicidal capsule. Most subsequent authors have agreed with this treatment, and generally the Clethraceae have been considered to be primitive members of the Ericales. However, recent authors have suggested that certain of the characteristics of *Clethra* which are often considered as primitive, may be derived. Among these Copeland (1943) included the tricarpellate ovary with loculicidal dehiscence, and Kavaljian pointed out that the corolla of separate petals may be a derived condition in the Clethraceae, as was previously suggested for this condition in the Pyroleae and Monotropoideae by Copeland (1947). Also, the vascular supply to the sepals in the species of *Clethra* which have been studied show a single trace with a single associated gap, a condition generally considered to be derived, not primitive. The seeds

of *Clethra*, with seed coats only a single cell layer thick, also indicate a reduction.

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1. **Clethra** Linnaeus, Sp. Pl. 1: 566. 1753; Gen. Pl. ed. 5. 188. 1754.

Deciduous shrubs or small trees, leaves alternate, simple, obovate, ovate or oblong, with serrate margins. Flowers in terminal racemes or panicles, fragrant. Bracts subtending the flowers, lanceolate, caducous or persistent, usually dropping shortly after anthesis; densely clothed with stellate or simple trichomes or both. Pedicels ridged and somewhat flattened laterally, increasing considerably in length during the maturation of the flower. Sepals 5, equal, quincuncially imbricate (with 2 sepals that are totally external, 2 totally internal, and 1 with 1 edge external and 1 edge internal), united at the extreme base, free above, lanceolate, elliptic, or ovate, the apex acute or obtuse, persistent in fruit. Petals 5, free, arranged in a quincuncial pattern in bud, spreading apart at anthesis, white or occasionally pinkish, alternate with the sepals, glabrous [ciliate margins], obovate or obovate-elliptic. Stamens 10, in 2 whorls of 5, the outer whorl opposite the petals, arising at a slightly lower level and often somewhat shorter than the inner whorl which is opposite the sepals; filaments glabrous or pubescent, somewhat flattened, laterally expanded and adnate to the corolla at the extreme base; anthers extrorse in bud, becoming inverted and introrse at anthesis by a straightening of the filament, 2-lobed, sagittate, the lobes separate above the middle for about one-half their length, but remaining together below the middle, becoming attenuate toward the base, the two thecae of each lobe becoming confluent shortly before the

pollen is shed, dehiscing by means of apical (morphologically basal) pore-like slits; pollen grains single, tricolporate. Gynoecium syncarpous, pubescent to hirsute, ovoid to subglobose, with a small depression at the apex at the point of connection with the style; 3-locular, each locule containing a single, pendent, placental arm which arises from a central column of tissue extending longitudinally from the receptacle to near the apex of the ovary; ovules numerous, small, anatropous, borne on the outer surface of the placental arm; style single, cylindrical, dividing near the apex into 3 lobes which are stigmatic at their tips, shorter than the stamens at anthesis, becoming equal to or longer than the stamens shortly after anthesis. Fruit a globose or subglobose, 3-lobed, 3-valved, loculicidal capsule, more or less inclosed at maturity by the persistent calyx. Seeds numerous, small, irregularly ovoid [occasionally winged], with very thin seed coats. TYPE SPECIES: *C. alnifolia* L. (Name Greek, *Clethra*, alder, alluding to the resemblance of the leaves of the type species to those of an alder.) — SWEET PEPPERBUSHES.

A genus of 30–40 species, represented in our area by only *Clethra alnifolia* L., *C. acuminata* Michx., and *C. tomentosa* Lam. *Clethra tomentosa*, treated by some authors as a variety of *C. alnifolia*, differs from that species in having leaves that are densely tomentose on the lower surface and sepals that are longer and obtuse, rather than acute.

De Candolle divided *Clethra* into two sections: EUCLETHRA (§ *Clethra*) with exserted stamens and styles, and CUELLARIA, with included stamens and styles. Drude described a third section intermediate between these to include a single species, *C. arborea*, with stamens included but with the style exserted. Hu, in a revision of the Chinese species, added still another section, again to include only a single species, and divided sect. CLETHRA (§ *Euclethra* DC.) into four series. According to this scheme, the species in our area belong in sect. CLETHRA, ser. *Alnifoliae*.

In common with a majority of the Ericales, species of *Clethra* are usually found growing in acid soils. *Clethra alnifolia* is distributed in acid swamps and low, moist woods and pinelands along the Coastal Plain from Maine to Texas, with occasional extensions into the Piedmont, particularly in the Carolinas. *Clethra tomentosa* (or *C. alnifolia* var. *tomentosa* Michx.) is more restricted, occurring only on the Coastal Plain from southern North Carolina to Louisiana. The two thus overlap geographically in this area. *Clethra acuminata*, distinguished from the other species in our area in having oval or oblong, acuminate leaves, solitary racemes, and pubescent filaments, is geographically isolated from the other species, occurring on the Appalachian Plateau and inner Piedmont, from southern West Virginia to northern Georgia.

Chromosome numbers have been reported by Hagerup for *C. arborea* ($n = 8$), and *C. alnifolia* ($n = 16$). Other genera of the Ericales for which a base number of 8 has been reported are *Calluna* and *Monotropa* in the Ericaceae (Hagerup, Löve & Löve) and *Melichrus* in the Epacridaceae (Smith-White). Several other genera of the Epacridaceae, however, have

been reported to have a base number of $n = 4$, which could easily be the original base number for the Clethraceae.

FIG. 2. **Clethra.** *C. alnifolia*: a, flowering branchlet, some leaves and racemes removed, × ½; b, flower, × 3; c, d, anthers, inner and outer views, × 15; e, ovary and base of style in vertical section, diagrammatic, stylar canal in black, × 15; f, ovary, diagrammatic cross section, × 15; g, mature capsule, seeds shed — note persistent placentae, × 8.

The unusual structure of the stamens in the Clethraceae has been the subject of considerable discussion, and there is still no universal agreement as to whether the anther is in the normal position in bud and inverted at anthesis or vice versa. A majority of recent authors is of the opinion that the anthers are inverted at anthesis, so that the apparent apex is the morphological base. This interpretation, which is that followed in the present treatment, is based on the pattern of the vascular trace in the anther. At anthesis, the stamen trace bends downward just beyond the point at which it enters the anther. There is, however, a small extension of the trace which continues upward in the connective tissue for a short distance. In the normal pattern of stamen vascularization, in taxa in which the stamens do not undergo a 180° rotation, the stamen trace passes longitudinally through the anther toward the apex. A pattern similar to this is found in the stamens of *Clethra* before anthesis. Thus

the anther is interpreted as being in the normal position in bud and inverted after anthesis. Hu disagrees, stating that the 180° rotation of the anther is merely the result of a straightening of the filament, and only after the filament has straightened is the anther normally oriented. In this connection, she suggests that the anther rotation is comparable to the unfolding or unrolling of a leaf.

Several species of *Clethra*, including the three species in our area, are cultivated as ornamentals in many parts of the world. They are easily propagated either by seeds or by soft-wood cuttings. The cultivated species are prized for the spicy fragrance of their blossoms, and for their mid- or late-summer flowering period — a time when few plants are in flower. *Clethra alnifolia* f. *rosea* Rehd., a pink-flowered form which occurs sporadically in the wild, is commonly found in cultivation.

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STUDIES IN THE GENUS COCCOLOBA, XI. NOTES ON THE SPECIES IN ASIA

Richard A. Howard

The genus *Coccoloba*, as recognized today, is native only in the Western Hemisphere, although several epithets in the genus, based on specimens from Asia, were published in the eighteenth and nineteenth centuries. All of these, however, either have been referred to other genera of the Polygonaceae or represent *nomina nuda* which cannot be identified. A few species of *Coccoloba* have been introduced into cultivation in Asia, and *C. uvifera,* at least, has become established in several areas.

The following species were described and based on specimens from Asia. I have not examined the types of any of them.

Coccoloba adpressa Meisner ex Steudel, Nomencl. ed. 2. 1: 390. 1841.

Steudel attributed to Meisner the combination *Coccoloba adpressa* (Labill.) Meisner, based on *Polygonum adpressum* Labillardière (Nov. Holl. Plant. Spec. 1: 99. *fig. 127.* 1804). Meisner, however, referred to the species as *Muehlenbeckia adpressa* (Plant. Vasc. Gen. 2: 227. 1840) and it is so treated in modern Australian floras.

Coccoloba asiatica Loureiro, Fl. Cochinch. 239. 1790.

Jackson (Index Kewensis 1: 573. 1895) referred this name to *Polygonum asiaticum.* In a study of Loureiro's work, Merrill (Trans. Am. Philos. Soc. II. 24: 143. 1935) stated that Loureiro "described the same species twice under *Coccoloba, C. asiatica* . . . and *C. cymosa* . . ." Merrill referred both species from Cochinchina to *Polygonum chinense* L.

Coccoloba australis Forster, Prodr. 29. 1786.

The Forster specimen from New Zealand was transferred to *Muehlenbeckia* by Meisner (Plant. Vasc. Gen. 2: 227. 1840). This genus has been conserved, with *M. australis* (Forst.) Meisn. designated as the type species.

Coccoloba chita ? (Hort.), Cat. Pl. Hort. Bot. Bogor. 91. 1866, nomen nudum.

This epithet, published without description, was not included in later editions of the catalogue. No material bearing this name has been preserved.

Coccoloba crispata Buchanan-Hamilton in Roxburgh, Fl. Ind. 2: 292. 1832.

Meisner (DC. Prodr. **14**: 130. 1856) listed this species with question in the synonymy of *Polygonum chinense* L. var. *thunbergiana* Meisner. He gave credit for this placement to Wallich in notes on record in the Griffith herbarium. Hooker (Fl. Brit. Ind. **5**: 45. 1886) accepted the synonymy under *P. chinense* without question. The original description stated that the plant is a native of Nepal and was growing in the Botanic Garden at Calcutta.

Coccoloba cymosa Loureiro, Fl. Cochinch. 240. 1790.

Jackson (Index Kewensis 1: 573. 1895) referred this epithet to *Polygonum cymosum* without citing an author for the latter name, but Index Kewensis lists *Polygonum cymosum* Roxburgh, Hort. Beng. 88. 1814 [*nomen nudum*] and Fl. Ind. 2: 289. 1832 (which has been referred to *P. chinense* L.), as well as *Polygonum cymosum* Treviranus, Nov. Act. Nat. Cur. 13: 177. 1866, referred to *Fagopyrum cymosum* Meisner. Merrill (*loc. cit.*) concluded that the Loureiro species was to be associated with *P. chinense* L.

Coccoloba dubia Hort. ex Trimen, Hort. Zeyl. 67. 1888, nomen nudum.

No specimens are available to document this name which has not been uesd in more recent literature.

Coccoloba indica Wight ex Meisner in DC. Prodr. **14**: 131. 1856, pro syn.

Lindau (Bot. Jahrb. **13**: 220. 1890) listed "*C. indica* mss." in a collection of excluded species at the end of his monograph. He failed to acknowledge that earlier Meisner had cited this manuscript name, attributed to Wight, in the synonymy of *Polygonum chinense* L. var. *ovalifolium* Meisner.

Coccoloba platyclada (F. Mueller) F. Mueller, Bot. Mag. **89**: *pl. 5382*. 1863.

Mueller originally described *Polygonum patycladum* [sic] (Trans. Phil. Inst. Vict. 2: 73. 1858) and later sent to Hooker, for publication in the Botanical Magazine, an excellent drawing and description. Since Hooker added only two lines of commentary, he should not be considered the author of this combination or of the article, as he is frequently cited. Mueller corrected the obvious typographical error in the specific name in synonymy and transferred the species to *Coccoloba*. Meisner (Bot. Zeit. **23**: 313. 1865) considered the species as "*Muhlenbeckia platyclados*" and

many modern floras use the epithet *Muehlenbeckia platyclada*. Bailey (Gentes Herb. 2: 58. 1929) discussed the generic limits involved and established a former section of the genus *Polygonum* as the new genus *Homalocladium* for the species.

The original publication data attributed the plant collection to Shepherd from New Caledonia. In the Botanical Magazine (*loc. cit.*) Meisner clarified the origin by commenting, "This remarkable plant was discovered at Wanderer Bay, Solomon's Islands, by Mr. Milne, during Captain Denham's Voyage of H.M.S. Herald, and a living specimen of it was communicated to Messrs. Shepherd, of the Darling Nurseries, of Sydney, from whence the plant was received at the Melbourne Botanic Garden."

Coccoloba totnea Buchanan-Hamilton in D. Don, Prodr. Fl. Nepal. 75. 1825.

Hooker saw the Hamilton specimen and referred the species to the synonymy of *Polygonum molle* D. Don (Fl. Brit. Ind. **5**: 50. 1886). Danser (Bull. Jard. Bot. Buitenz. III. **8**: 233. 1927) referred both species to the synonymy of *P. paniculatum* Blume.

INTRODUCED SPECIES

Coccoloba caracasana Meisner in DC. Prodr. **14**: 157. 1856.

A specimen was received from Dr. Otto Degener (*s.n.* [A]) who reported that the species was being used as a hedge on the campus of the University of Hawaii, Honolulu, Oahu.

Coccoloba uvifera (L.) Linnaeus, Syst. Nat. ed. 10. 1007. 1759.

The common sea grape has been introduced as an ornamental shrub or tree for seaside plantings in many islands of Polynesia, and on Kauai, in Hawaii, I have observed plants which, having persisted after cultivation, are becoming established spontaneously. The following references are to *Coccoloba uvifera* in the Pacific area: Rarotonga (Wilder, Bishop Mus. Bull. **86**: 47. 1931) Nuku Hiva, Marquesas (Brown, *ibid.* **130**: 67. 1935); Vaitepaua, Makatea (Wilder, *ibid.* **120**: 21. 1934); Batavia, Java (Danser, Bull. Buitenz. Bot. Gard. III. **8**: 241. 1927). I have seen the following specimens:

Hawaii. OAHU: *Degener 8986* (NY), *Thompson s.n.* (NY). **India.** Calcutta, cult. Calcutta Bot. Gard. *s.n.* (NY). **Indochina.** Hanoi, Tonkin, *Petelot 3979* (NY); Saigon, *Poilane 2435* (A, NY). **Indonesia.** Bogor, *Wurjantoro 1* (A). **New Caledonia.** Noumea, *Franc 1320* (A, NY). **Tuamotu.** Makatea, *Wilder s.n.* (NY).

SCHIZOCARDIA BELIZENSIS: A SPECIES OF PURDIAEA (CYRILLACEAE) FROM CENTRAL AMERICA

JOAB L. THOMAS

ABOUT THIRTY YEARS AGO specimens of an unusual and very distinctive tree were collected in British Honduras by William A. Schipp and sent to the Field Museum of Natural History. It soon became evident that this tree was unknown in the Central American flora, and the specimens were eventually distributed under a provisional name as a new genus and species, *Schizocardia belizensis*, without any indication of relationship. Later, Smith and Standley (1932) described the plant under this name as representing a second genus in the Clethraceae, a relationship suggested by the collector.

Recently, Dr. C. E. Wood suggested that I look at specimens of *Schizocardia*, indicating that the plant resembled members of the Cyrillaceae. Examination of these specimens revealed that this plant fits well within the logical generic limits of *Purdiaea*, in the Cyrillaceae, and that it should be transferred to that genus.

Purdiaea belizensis (Smith & Standley) Thomas, comb. nov.

Schizocardia belizensis Smith & Standley, Trop. Woods **32**: 9. 1932.

DISTRIBUTION. **British Honduras.** Dist. Stann Creek: Nineteen Mile, Stann Creek Valley, *W. A. Schipp 965* (type, F; isotypes, A, GH); near Middlesex *W. A. Schipp 443* (A, F); Silk Grass Creek Reserve, *P. H. Gentle 2987* (A); Cockscomb Branch, *D. Stevenson 4* (F); Temax-Sarstoon, *N. S. Stevenson 164* (F). **Guatemala.** Dept. El Petén: northeast of Poptún, *F. B. Lamb 96* (F).

Characteristics of this plant which place it in the genus *Purdiaea* and exclude it from the Clethraceae are as follows: a greatly exaggerated quincuncial type of sepal insertion, with the exterior sepals considerably larger than and completely inclosing the interior sepals; an ovary composed of 5 carpels and 5 locules, with each locule containing a single, pendulous ovule; a single style with an unbranched stigma; and a dry, indehiscent fruit which is usually devoid of seeds. The pollen grains, also, are almost identical in shape, size and structure to those of other species of *Purdiaea*. The Clethraceae, represented by the single genus *Clethra*, is characterized by equal sepals, a 3-carpellate, 3-locular ovary with numerous ovules in each locule, usually a 3-lobed stigma, and a loculicidal capsule with numerous small seeds.

The Cyrillaceae and the Clethraceae have many characteristics in common, however, and of the three genera in the Cyrillaceae, *Purdiaea* appears to be the one most closely related to the Clethraceae. The inclusion of a

species of *Purdiaea* in the Clethraceae is a further indication of the close relationship between these two families.

Purdiaea belizensis differs from other members of the genus in having distinctly laciniate sepals and axillary racemes. In all other known species of *Purdiaea* the sepals are entire, and in the specimens which I have examined the inflorescence is a terminal raceme. However, in *Cliftonia monophylla* (Lam.) Britton ex Sarg., of the Cyrillaceae, both terminal and axillary racemes have been observed, and it is not improbable that this situation also obtains in some species of *Purdiaea*.

The present species is very distinct, and its relationships with other species of *Purdiaea* are obscure. It seems to be most closely related to the South American *P. nutans* Planch., particularly on the basis of its scarious sepals and leaves with uniformly pinnate venation. The latter character was previously thought to occur in *Purdiaea nutans* only (Thomas, 1960). In size and shape of the leaves and the sepals and in general aspect *Purdiaea belizensis* also resembles *P. nipensis* Marie-Vict. & Leon. The latter species seems to be the nearest connecting link between *P. cubensis* (A. Rich.) Urb., of Pinar del Río, and the other Cuban species of *Purdiaea*, all of which are restricted to Oriente Province. Thus, in some respects the present species is intermediate between two groups of species, with *P. nutans* and *P. cubensis* forming one group, and the species in Oriente Province forming the other (*loc. cit.*, p. 45, *fig. 23*).

The recognition of a species of *Purdiaea* in British Honduras and Guatemala is particularly interesting in terms of the geographical distribution and relationships within the genus. Previously, the genus was known only from Cuba and northern South America, and the South American species seemed to be most closely related to the species from Pinar del Río. This seemed backward, at first, in terms of the logical distribution pattern, but the recognition of *Purdiaea belizensis* in Honduras and Guatemala adds further evidence to substantiate this relationship. Thus, *Purdiaea* becomes another of an increasingly large number of plant groups distributed in northern South America, British Honduras and vicinity, and the West Indies.

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STUDIES IN THE THEACEAE, XXXI
A NEW SPECIES OF ADINANDRA FROM THE CELEBES

CLARENCE E. KOBUSKI

Adinandra eymae, spec. nov.

Arbor vel frutex (habitus ignotus). Ramuli teretes, glabri, ut videtur rubro-brunnei; gemmis terminalibus conicis, glabris. Folia coriacea, glabra, obovata vel oblongo-obovata, 5.5–8.5 cm. longa, 2.5–3 cm. lata, supra brunnea (in siccis), subtus castanea, punctata, apice obtusa, rotundata vel emarginata, basi cuneata, margine integra, venis 8–10 paribus subtus obscuris, costa supra canaliculata, subtus elevata, petiolis ca. 3–5 mm. longis. Flores solitarii; pedicellis teretibus, glabris, 1.5–2 cm. longis; bracteolis 2, persistentibus, glabris oppositis vel subopppositis, inaequalibus, late ovatis, 3 mm. longis × 4 mm. latis et 4 mm. longis × 5 mm. latis; sepalis 5, imbricatis, inaequalibus, rotundatis, crassis, duobus exterioribus ca. 8 ×8 mm., tribus interioribus ca. 9–10 mm. longis, ca. 9 mm. latis; petalis 5, membranaceis obovatis, inaequalibus, apice rotundatis, duobus exterioribus 8–9 mm. longis, 5–6 mm. latis, tribus interioribus 9–11 mm. longis, 7–9 mm. latis; staminibus ca. 35, 1-seriatis, 5–6 mm. longis, filamentis inaequalibus, 2–3 mm. longis, pubescentibus, ad basim corollae adnatis, antheris glabris, aequalibus, ca. 3 mm. longis, connectivo pubescente; ovario globoso, glabro, 3–5 mm. longo, ca. 5 mm. diametro, 5-loculari, multiovulato, apice abrupte in stylo attenuato, stylo integro, glabro, ca. 3 mm. longo, stigmate capitato-punctiformi, indistincte 5-lobo. Fructus non visus.

Celebes: Subdivision Enrekang, between Pintealon, Pokapindjang and Tinabang, on ridge, alt. 2600–3000 m., *P. J. Eyma 588* (A, type; L, isotype), June 16, 1937 (buds cherry-red).

The striking feature of this species is the complete glabrosity throughout the whole plant, except for the pubescence on the stamens, a feature which immediately associates it with the genus *Adinandra*. The closest relative is undoubtedly the widespread *A. dumosa* Jack, so far unreported from the Celebes, although recorded as distributed from the Malay Peninsula south into Indonesia, Sarawak and British North Borneo. In *A. dumosa*, the corolla lobes are much longer (up to 16 mm. long), connate 3–5 mm. at the base and bluntly acuminate at the apex. The stamens are nearly twice as long, measuring up to 12 mm. in length, and the style may measure up to 15 mm. long, easily five times the length of that found in *A. eymae*.

In general appearance, the specimen cited above agrees very well with *Eyma 613,* a fruiting specimen of *Ternstroemia* collected the same day at the same locality. Eyma, the collector, undoubtedly thought that he had collected flowering and fruiting material of the same species (I did also), since he labeled them both *Ternstroemia*. However, on dissecting the flowers of *Eyma 588,* the type of this species, one finds that the ovary is five-loculate with many minute ovules in each cell, the placentation is parietal, and the stamens are hirsute. The terminal bud is conical. All these are generic characters used to separate *Adinandra* from *Ternstroemia*.

It is a pleasure to dedicate this species to the memory of the collector, Pierre Joseph Eyma, a promising botanist whose life ended so tragically in a Japanese prisoner of war camp near Palembang, Sumatra, on July 25, 1945.

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THE BOTANICAL RESULTS OF THE U.S. COMMISSION OF INQUIRY TO SANTO DOMINGO IN 1871

RICHARD A. HOWARD

IN THE GRAY HERBARIUM there is a small collection of specimens which were prepared by Charles Wright, C. C. Parry, and H. Brummel during a difficult period of United States-Latin American relations nearly a century ago. The specimens bear little information beyond the name, and yet approximately forty of these are "new species" which were never published. Supporting this collection is a 130-page handwritten manuscript entitled "Flora Domingensis" and attributed to Asa Gray and Charles Wright. This, too, was never published, although with a revision of only a few pages, the manuscript, with Latin descriptions of the new species, geographical localities, and dates would have been ready for the printer. One wonders why the manuscript prepared with such care was not published; why the specimens with incomplete labels and often conflicting numbers were so haphazardly distributed to herbaria; why two such competent collectors as Wright and Parry left so little record of their expedition together; and who was the botanist H. Brummel, who is today unknown among the collectors of West Indian vegetation.

Asa Gray, in a necrology of Charles Wright (Am. Jour. Sci. 31: 17. 1886) states, "The small collection made in this, his last distant botanizing, was not of much account." Parry's biographers refer to the Santo Domingo trip as a not very successful expedition, and Urban states (Symb. Ant. 3: 143. 1902) that the botanical results of this expedition made during an unfavorable part of the year and on a hasty trip were not outstanding. These comments seem inappropriate when applied to an expedition in an area which later yielded hundreds of new species to Eric Ekman; to a collection of nearly 700 numbers; and to a manuscript which might have been one of Charles Wright's outstanding publications.

From many sources, particularly the letters of Wright, Gray, Torrey, and Oliver in the historical files of the Gray Herbarium, it has been possible to piece together notes and comments to supply this documentation of the botanical results of the U.S. Commission of Inquiry. I am grateful to Dr. Reed Rollins, director of the Gray Herbarium, for permission to publish this report on an historical document in the Gray Herbarium files;

to Mrs. Lazella Schwarten, librarian of the Gray Herbarium and the Arnold Arboretum, who has been most helpful in tracing missing items; to Dr. John Reeder, of Yale University, who located Wright, Parry and Brummel collections in the D. C. Eaton herbarium, and, finally, to Mrs. Katherine Hall and Mr. Theodore Dudley for their assistance in methodically leafing through herbaria to locate the general collections cited. Many others in the United States and abroad have assisted and their help has been appreciated.

This study developed in the course of work on a flora of the Lesser Antilles through a consideration of certain species which occur in that area. This floristic project is supported by grant G-4441 from the National Science Foundation and for this assistance grateful acknowledgement is made.

HISTORY OF THE COMMISSION OF INQUIRY

The island of Hispaniola, comprising the countries of Haiti and Santo Domingo (now the Dominican Republic), lies in an important position in the Caribbean. In the 19th century, at the time of the Commission of Inquiry, it was subjected to the interests of European countries and was torn by internal strife. There was a desire on the part of some groups in Hispaniola and of many parties in the United States for the annexation of the country to the United States. Negotiations for annexation had been carried on during the administration of President Andrew Johnson (1865–1869) to bring about at least the acquisition of Samaná Bay to serve as a strategic naval station — a guard post for the Mona Channel, the gate to the Caribbean sea and the Isthmus of Panama. Soon after the inauguration of President Grant in 1869, the question of annexation was revived. The government of Santo Domingo sent an envoy to President Grant to solicit his consideration in the matter of Dominican affiliation with the United States. To ascertain the true state of affairs on the island Grant dispatched General Orville Babcock as a confidential agent to Santo Domingo. From Babcock's report Grant became convinced, first, that what had seemed a fabulous account of agricultural and mineral resources was true; second, that it would be advantageous to obtain Santo Domingo because of its value as a mercantile and naval station; third, that the people of Santo Domingo truly were desirous of their country's annexation to the United States; and finally, that by annexing Santo Domingo it would be possible to strengthen the Monroe Doctrine, since Santo Domingo thus would avoid domination by European powers. Working from these premises, Grant set about to have passed a treaty for the annexation.

Grant's efforts met with bitter opposition from European traders who wished to monopolize the Dominican trade, from the aggressive Negro party in Hispaniola which hoped to gain control over the established Dominican government, as well as the entire island, and from some American groups whose spokesman, Charles Sumner, led the fight against annexation. When Babcock's reports were challenged, Grant established

through an act of the U.S. Senate a new party of investigation. The Commission was headed by Dr. Samuel Howe, a noted philanthropist, Benjamin Wade, a former senator, and Andrew White, the president of Cornell University. These three, with their supporting assistants, secretaries and scientists, called themselves the U.S. Commission of Inquiry to Santo Domingo. They visited Santo Domingo during the latter part of January through early March, 1871, and submitted their report, which was published as the Executive Document 9, 42nd Congress, 1st Session, 1871. The goal of the Commission was to survey the natural resources; the nature of the health, education, and government of the people; the nature of foreign claims to the area; and the attitude of the people to annexation. These goals were met fully. Although the report for the most part supported the idea of annexation, the proposal itself was defeated in the U.S. Senate. In due time even the lease on Samaná Bay was abandoned, and some years later a naval base was established in Guantanamo Bay, Cuba, as an adequate substitute.

ACTIVITIES OF THE COMMISSION

The Commission of Inquiry consisted of twenty-two official representatives traveling at government expense and ten representatives of the press who were given transportation. The scientists, in the order and with the title given in the official report, were: Prof. W. P. Blake, geologist and mineralogist; Prof. C. C. Parry, botanist; Dr. W. Newcomb, naturalist; A. R. Marvine, assistant geologist and mineralogist; E. Waller, assistant mineralogist and chemist; J. S. Adam, assistant mineralogist and chemist; Prof. H. A. Ward, zoologist and paleontologist; C. Wright, botanist; and H. Brummel, botanist. There is no information on how these men were selected, but it is apparent from the titles throughout the report that Parry was considered to be the principal botanist and that Wright and Brummel were considered as aides. At the time of the expedition, Parry was not a professor but was officially botanist for the U.S. Department of Agriculture, having been appointed to that post in 1868. Brummel apparently was an employee of the Department of Agriculture, and nothing can be found on his professional career either prior to or after the trip. Charles Wright, well known as a botanical collector, had completed his last trip to Cuba in the summer of 1867 and was operating a farm in Wethersfield, Connecticut, during the summers and working as an assistant to Asa Gray, at the Gray Herbarium in Cambridge, Massachusetts, in the winter. Both Parry and Wright were well known to Gray, and it is possible that he suggested Wright for the trip. Wright was 60 years old and in poor health at the time of the expedition, and one wonders what inducement led him to join the Commission.

The large number of reporters accompanying the Commission indicates the delicate nature of the investigations and the interest of the newspapers and the public in their findings. There is even a suggestion of intrigue in the official report of the trip. The assistant to the confidential secretary

of the Commission was discharged and sent back to New York, with the note being made in the report that this man had misrepresented himself and was, in fact, an assistant editor of an important New York newspaper. Although the reporters were supposed to be observers, the Commission delegated several of them to make special trips to gather information, with power to conduct interviews on behalf of the Commission. Letters from these reporters were published in many papers in the United States while the expedition was in the field. Feeling about the trip and the principle of annexation was high in the United States. John Torrey and Asa Gray, both to be involved in an aftermath of the Commission's trip, expressed opinions against the principle of annexation of Santo Domingo.

The Commission left New York on January 17, 1871, aboard the U.S. Steam Frigate "Tennessee" heading for Santo Domingo City. Supplies of coal ran low en route, and, on January 24, the "Tennessee" stopped in Samaná Bay, where it was joined by the cutter "Nantasket." Coal had been reported along the shores of Samaná Bay, but on investigation this proved to be a low-grade lignite. While at anchor in Samaná Bay, the Commission and its scientists were divided into parties with different assignments. One party investigated the shoreline and the anchorage of the bay, while another went to the interior of the Samaná peninsula. A third party was sent overland to Santo Domingo City with a message for the secretary of foreign affairs to announce the impending arrival of the "Tennessee" and the Commission in the capital. Still another group was sent overland to the capital to investigate the resources en route, and a last party was sent to Puerto Plata by the north coast. The "Tennessee" remained in Samaná Bay until January 29th, when it departed for Santo Domingo City, arriving there on the 31st.

On January 26th, the Commission resolved "that the botanists attached to the expedition be requested to examine and report to the Commission regarding the trees, plants, roots, and grains and their vegetable products of that part of the island adjacent to the Bay of Samana, especially with regard to such trees and plants as may be of commercial value, or in any way decidedly useful to man." According to the published report, Parry was the botanist to make this trip in a party headed by the geologist Blake. Contrary to the report, Wright's letters to Asa Gray (January 31, 1871; February 5, 1871) indicate that he also made this trip. The party left the anchorage off Samaná on January 26th and proceeded to Punta Corozos, Punta Mangle, Punta Grigri, Los Róbalos, Cabeza de Toro, and Santa Capuza, where they spent the night. On January 27th the party visited Punta Gorda, where they investigated the reported coal seam, and then proceeded to Canitas, the mouth of the Yuna river, and back to Cabeza de Toro for a night anchorage. The following day, January 28th, the Blake party visited Punta Corozos and returned to the "Tennessee" off Samaná. Parry wrote the official report of this trip entitled "Report on the botanical features, agricultural products and timber growth of the peninsula of Samana." In it he described the cultivated crops, grasses, fibers, fruits, palms and timber trees. He also stated, "The short interval allowed for

botanical examinations on the peninsula of Samana has been improved by a very fair local collection of plants numbering about two hundred species."

On January 27th, while Parry and Wright were in the field, the Commission resolved that Prof. Ward, the zoologist, make a trip along the coast in the direction of Cape Cabrón, "not exceeding ten days," and then go by land to Santo Domingo City "making a tour not exceeding a week," and that "Professor Wright and Mr. Brummel be requested to accompany Professor Ward, in order to complete the examination of the vegetable products of the peninsula." According to the official report, this party departed before Parry and the Blake party returned. Again, Wright's letters to Gray are in conflict with the published report, for Wright wrote that he sailed with the "Tennessee" and collected in the vicinity of Santo Domingo City while Brummel was traveling overland with Ward.

The Ward expedition left the Samaná anchorage and spent January 29th and 30th at Punta Cacao. They were prevented by high seas from rounding the tip of the Samaná peninsula and landed instead at "Port Francais" (Jan. 31) and went inland to Las Galeras and the Bahía del Rincón, returning to "Port Francais" the following day, February 1st. If this part of the report is true, it must have been a difficult and rapid trip and not a collecting expedition. On February 2nd, Ward and party, with Brummel along, crossed Samaná Bay, stopping at Cocal San Lorenzo. There are two specimens in the Wright, Parry and Brummel series attributed to San Lorenzo and these must have been gathered by Brummel. The party was in Savana de la Mar on February 3rd and then proceeded up the Yuna river on February 4th and 5th to Almacen (February 6th). They traveled overland to San Francisco de Macoris and on to La Vega and Cotui, all on February 7th, and on to Cevicos (February 8th), through the mountains of eastern Hispaniola to Savana la Grande, and arrived at Santo Domingo City on February 9th.

Meanwhile aboard the "Tennessee," anchored in very rough waters off Santo Domingo City, on February 4th the Commission asked Blake to make geological investigations about the capital and to organize an expedition to cross the central range of mountains to Puerto Plata, in a period not to exceed two weeks. Wright was to accompany him and to report on the vegetation of the interior. In the same resolution Parry was directed to examine the area around Santo Domingo City and to report. Wright's letters reveal that Parry was still suffering from a cold and that Wright took extended walks around Santo Domingo City; his letters describe the vegetation in considerable detail. On February 8th the report reveals that Blake accepted the directive to cross the island but that the time allotted was extended and the rendezvous time in Puerto Plata was set for March 1st.

On February 9th the botanists attached to the Commission were literally going in all directions. Parry and members of the Commission were on a leisurely trip by boat fifteen miles up the Río Ozama and then another 15 miles up a branch to the westward before returning in the late afternoon. Wright's letters and notes indicate that his party headed westward to the

Río Haina to begin a trek across the island. Brummel and party returned to Santo Domingo City on that day and apparently remained aboard the "Tennessee" to write up their report entitled, "Notes on the agricultural resources of Samana Peninsula and the Vega Real." There is a suggestion that Brummel did not collect botanical specimens on his trip with the Ward party, and his report is in contrast to others published. It is written in the most general terms and contains only one botanical scientific name. Brummel's name does not appear again in the official report of the activities of the Commission.

While the Blake party, including Wright, left Santo Domingo City to make their way to Puerto Plata, the Commission, with Parry and Brummel, remained in Santo Domingo City and concluded its work. The cutter "Nantasket" left the capital anchorage on February 14th for Puerto Plata, where some members of the Commission were to proceed inland to La Vega, meet the Blake-Wright party in Puerto Plata on March 1st and then rendezvous with the "Tennessee" at Port au Prince on March 7th. Other members of the Commission, with Parry and apparently Brummel on board, sailed with the "Tennessee" on February 14th, arriving at Ocoa Bay on the 23rd. Members of the Commission went inland to the town of Azua, and the "Wright, Parry and Brummel" specimens from Azua must have been collected by Parry or possibly Parry and Brummel during that visit. The "Tennessee" left Ocoa Bay on February 28th and arrived at Port au Prince on March 9th.

WRIGHT'S TRIP FROM SANTO DOMINGO CITY TO PUERTO PLATA

Wright's manuscript of the "Flora Domingensis" carries many references to plants collected at "interior savannas," "wet vallies of the interior," "pine woods of the interior," most with dates of collections and a few plants with specific geographical locations. The official report, however, gives barometric readings with dates and places. It is possible to coördinate these two sets of data to derive the following itinerary of the crossing of Hispaniola.

February 9, Santo Domingo City, Río Haina, Santa Rosa, Arroyo Lebrun.
February 10–11, Madrigal.
February 12, Arroyo Los Guananitos, La Puerta.
February 13, Loma Laguneta, El Aguacate.
February 14, Río Maimon, Hato del Banao.
February 15, Arroyo Yuma, Río Yuna, Río Jima.
February 16, La Vega.
February 17, La Vega.
February 18, Santo Cerro.
February 18–19, Moca.
February 21–25, Santiago (February 23, Río Yaqui del Norte).
February 26–28, Arrenquillo River, El Limón, Loma de Bajabonico.
March 1–3, Puerto Plata.

Even with modern roads, this trip of about 105 airline miles would be an arduous one by foot or by horseback. In 1871, with few established paths, these deep with the mud remaining from the rainy season, it was an heroic undertaking in the time allotted for the 60-year-old Wright. A reporter who had come by boat to Puerto Plata to visit La Vega commented, "The only road from Puerto Plata to the interior is a bridle path to Santiago. In a direct line Santiago is only 18 miles, but by path it is 60 miles." He comments that the rainy season was scarcely over and that the paths were muddy and slippery. On his arrival in Puerto Plata, Wright received instructions to report on his trip immediately. His pique clearly shows in the first paragraph of his report. "The journey was made at a season of the year when fewest plants are in flower and not many in fruit. Called to join this Commission almost at a moment's warning, no time was afforded to obtain books suitable or sufficient to determine the plants found there; and the only books brought were left on the ship from a desire to reduce the luggage to the smallest possible dimensions. Moreover, no time could be saved to examine the plants in their fresh state, and to study them carefully, without neglecting the specimens gathered, by the careful preservation of which they might be more critically examined at a future time. Even the inquiries for the vernacular names of trees met with received unsatisfactory answers. The muleteers and guide seemed to know few of the trees of the mountain regions. Even when inquiries were addressed to the inhabitants, answers, whether thoughtless or intentional, so absurdly wrong were given that I despaired of gaining much reliable information which would serve to connect with certainty the vernacular names of the plants with their scientific ones. A more particular report must consequently be postponed till a critical examination of the specimens can be made." This proved to be a forecast of trouble to come.

The rendezvous at Port au Prince between the "Nantasket" and the "Tennessee" occurred on March 9th. This date is also recorded as the departure date for Kingston, Jamaica, where the "Tennessee" arrived March 11th. The "Nantasket" apparently returned to Puerto Rico or to Saint Thomas. While the "Tennessee" re-coaled in Kingston harbor, Wright had the opportunity of visiting the government Forestry Station at Cinchona in the Blue Mountains. He refers in later letters to his knowledge of the growth of quinine trees in Jamaica. It was in this area that Wright must have collected an unnumbered specimen of *Vaccinium meridionale* (US) which has bothered monographers. The species is not known from Hispaniola but does occur in the vicinity of Cinchona.

From Jamaica the "Tennessee" proceeded to Charleston, South Carolina, arriving there March 26th. The Commission held meetings aboard the ship en route and on March 19th, while at sea between Cape San Antonio de Cuba and Key West, they resolved "that the collections made by the scientific gentlemen who have accompanied this expedition be inventoried by them and deposited in the Smithsonian Institution, subject to the disposition of Congress." That all was not harmonious in the acceptance of this resolution is attested by the comment in the official

report, "During the discussion of said resolution the Commission took a recess until 7 o'clock p.m." Whether Parry wanted the specimens for the herbarium in his charge at the Department of Agriculture or whether Wright felt his collections, or all of them, should come to the Gray Herbarium for his study can not be resolved. In any case, the issue was not settled amicably, as is obvious from a note in the official report regarding a meeting of the Commission at the Arlington Hotel, Washington, D.C., on April 3, 1871. It is noted there that the Commission "received the following letter dated April 3 from Joseph Henry, Secretary of the Smithsonian Institution: 'Sir: On reply to the inquiry you make as to the disposition of specimens collected at the expense or under the auspices of the United States Government, I have the honor to inform you that, by the law of Congress organizing the Smithsonian Institution, it is the official curator of all collections of natural history, geology, etc. belonging to the United States, and that in accordance with this enactment all the specimens collected by the Wilkes, Gilliss, Rodgers, Perry and other naval expeditions, and the Pacific Railroad Boundary and geological surveys, are now in its custody.

" 'I may further state that an annual allowance is made by Congress for the preservation and exhibition of these and such other collections as may be made, and also for the distribution of the duplicates to academies, colleges and public museums.

" 'I am, very respectfully, your obedient servant,' . . ."

Thus, at the end of the Commission's report, the fate of the collections, as well as the responsibility for working them up, remains unclear.

The "Tennessee" arrived at Charleston, South Carolina, on March 26th and put ashore the heads of the Commission and several of the scientists, including Parry, who went to Washington. Wright remained on board as the "Tennessee" sailed to the port of New York. John Torrey wrote about this trip to Asa Gray on April 1, 1871. "Wright made his appearance at the office about noon today. He came directly from the Tennessee — which has been ever since the Santo Domingo Commissioners were landed at Charleston in reaching New York. She had expended all her coal and was unable to get up from the Quarantine to the city. He was quite disgusted with the ship and the miserable quarters — or rather filthy den that they had put him in — it being the very worst in the whole vessel. H . . . took him out to dine and although he would take nothing but plain beefsteak said it was the best dinner that he had eaten since he left for S. Dom. This afternoon that good man (I do like him) left for Wethersfield. It will probably be some days before he goes to Cambridge — for his wardrobe needs replenishing and he wishes to attend to some matters at home." Torrey also added, "I have not heard from Parry since his return. It seems that he has all of Wright's S. Dom. plants as well as his own — and it is understood that you will have the bulk of the collections, although they are not very bulky." Later letters proved incorrect the implication in the last sentence that Parry then had in his possession the specimens collected.

CHARLES WRIGHT AND ASA GRAY

It is not clear when Wright returned to Cambridge, how the collections finally reached the Gray Herbarium, or, in fact, how it was determined that Wright was to identify the collections which were then to become the property of the Department of Agriculture.

On June 5, 1871, Gray wrote to Wright at Wethersfield, "Will you do up the San Domingo plants for 8 dollars a page? . . . If you come and set to work with me I shall be pleased & you shall take time to distribute your San Domingo plants. If you study them for Parry or Washington — that will take ½ your time for some months. But 8 dollars a page for 80 pages or so would fairly pay. What presses me most is work in the Garden seeing to things & names and I much wish you would take hold and help an over worked fellow."

It was during these months that Gray was deeply concerned over the condition of the Botanical Garden in Cambridge. Without adequate funds to employ the number, or even the quality, of people required by the garden, Gray was seeking the devoted individual who would work for the small sum of money available.

On June 8th, Gray wrote two letters to Wright. In the first he stated, "Nothing therefore was meant on my part but to tell you the coast is so nearly clear here that you could do something if you wished either for Herbarium or for San Domingo coll. on your own hook." In the evening Gray wrote again, "Dear Wright. Let me go on. My *bete noire* here is the garden," and he elaborated on the problems of financing the herbarium work and the care of the garden. He continued in the letter to Wright, "You prefer to be Herbarium Curator, and I wish I could keep an herb. curator pure and simple, and it is just in your way. But the Herbarium fund yields only 850 dollars which is nearly all needed to run the establishment. And I must pay for most of the aid I could get out of my pocket. I could do something that way, and I would, if only I had the Garden off my mind."

Apparently Wright misunderstood Gray's interest in giving the Garden primary consideration as some reflection on his own taxonomic ability, for Gray was forced to explain in a letter to Wright dated June 28th, "As to the way you are doing up Cuban Botany, I do not find fault with it. I think, with you, that you are doing about the best possible thing under the circumstances. The only thing that you may justly complain of me for, I think, is my sensitiveness and *pooh-poohing* new species making in families where the old species are yet all in a jumble and where I have thought that you could not yet tell what were new and what old. I dare say I have been too impatient about it, and I see I have hurt your feelings somewhat, which I am sorry for. I only meant: take time & pains to clear up the old ones in the books, and get a better assurance, if you can, about the proposed new ones. But, after all, it is wrong and foolish in me to worry myself, or you, about them.

"You will have more experience of the sort in the working up of your

San Domingo coll. But if we can get time to refer doubtful cases to say Oliver at Kew, and some one at Paris (where they have many old San Domingo plants), I suppose you may get them pretty straight.

"I suppose these collections will keep you pretty busy this summer. But I hope you can complete the incorporation of the Ind. Or. residue . . ."

Wright apparently was reassured, and he appears to have been working on the collections in the early fall of 1871.

THE FATE OF THE COLLECTIONS

Wright did not have the collections in his possession when he left the "Tennessee" in New York on April 1. On April 11, Parry wrote to Gray, "You will see Wright soon and get particulars. I do not think he was treated as his services deserved but perhaps Prof. White was not to blame. It was a badly arranged affair but Wright has at least the satisfaction of knowing that he did his duty faithfully and the results will show that he deserved better treatment. Our so called *assistant*? (Wright knows who I mean) neglected his duty to the last. I left him in charge of the heavy boxes on the ship to dry and he took the 1st. boat for land and they are still on the ship. Have written to the Agr. Dept. agent to hurry them off. This delays me sorting out the collection as I intended to do at once. Tell Wright to write me as soon as he arrives at Cambridge."

This letter suggests that all was not well on the expedition and that the relations between the "botanists" were not completely harmonious. Apparently Wright was mistreated and Brummel was not exactly an asset. The letter also suggests that Parry intended to sort out the collections. Since all the specimens I have seen bear labels stating, "Distributed by the U.S. Department of Agriculture," it is clear that the specimens did not go to the Smithsonian Institution at that time and that Parry must have had the labels prepared.

Although correspondence between Parry and Wright and Parry and Gray is referred to in many of Gray's letters, such letters are not available for reference. Gray did write to Charles Wright on June 8th of Parry's intended visit to Cambridge soon after the 20th and also reported that "your 2 S. Domingo boxes are in my back kitchen." Torrey's earlier comment suggests that the two boxes represent both Parry's and Wright's collections and that they were in Cambridge for study by Wright and Gray.

Wright apparently worked over the collection during the summer and early fall of 1871. One specimen from Azua was selected as an unnamed new genus and species of the Polygalaceae. Regrettably no specimens of this taxon were cited by number under the detailed description given in the "Flora Domingensis." I have been unable to find any specimens to which this description might refer in any American herbarium. In a letter dated September 15, 1871, Oliver, of Kew, wrote to Asa Gray, "I have delayed a few weeks in replying to your note with San Domingo fragment wishing to show it to Mr. Bentham before reporting. Unfortunately I have

little to tell. The free or possibly free stamens and anther cells make it awkward for the Polygalaceae which seems after all the best place for it. *Loxopterygium* and allied genera of the Sapindaceae won't do. I keep the scrap but will return it at a word from you." There is no way of knowing if the "scrap" was the entire specimen of the new genus or if any material was retained by Gray where it is filed. Gray acknowledged Oliver's letter on October 16, 1871. "Receive a hasty line to thank you in Wright's name for your report on the little San Domingo puzzle . . . tho you leave it a puzzle still. Keep the scrap. I send by the Darwin Junior, a small parcel for Herbarium chiefly San Domingo plants. There are 40 to 60 of these which are puzzles or dubious or 'n. sp.' of Wright — in whose determinations I have small confidence. But unless I can tell him what a thing is, I can rarely stop him from printing. Could you, as you lay out for the *Herb*. just report on them as far as you can, without too much trouble. I have never looked at one of them — no time.

"The collection as a whole is meagre & poor. But there are some things worth your having. I am going to take his collection and will send in any duplicates which you are likely to care for. The greater part are common tropical rubbish."

Oliver received this shipment in November, examined it and reported on a part of the collection in December. Gray, in turn, acknowledged Oliver's assistance in a letter of January 7, 1872.

The ferns and their allies from the collection were sent by Wright to D. C. Eaton, in New Haven, Connecticut. Eaton gave these plants his own set of numbers (1–38) and reported the identifications in a memorandum dated October 22, 1871. Wright's manuscript flora has incorporated both the Oliver and the Eaton determinations. The manuscript therefore must have been prepared in early 1872, for Wright returned to his Wethersfield farm for the spring plowing. On September 16, 1872, Wright wrote to Gray that he knew Sereno Watson was to be his successor, and, although he needed the employment and would sorely miss the income, he hoped Watson would be able to do the work well.

Wright died in 1885. Asa Gray reported in a necrology of Wright that after the Santo Domingo expedition, "a large part of several years was passed at Cambridge, taking part of the work of the Gray Herbarium; and one winter was passed at the Bussey Institution." I can find no records stating specifically why the manuscript was put aside and never finished. Wright's presence in Cambridge suggests there was an opportunity for him to complete it, but perhaps an explanation for his failure to do so can be found in other episodes which followed the completion of the Commission of Inquiry.

WRIGHT'S EXPERIENCES ON THE EXPEDITION

Torrey's letter to Asa Gray, previously quoted, suggested that Wright was mistreated on the expedition but that he did his job faithfully. Charles Wright wrote to Asa Gray on January 31, 1871, and February 5, 1871,

from Santo Domingo. In these letters are bits of information which explain Torrey's comments, as well as some of the episodes which occurred after the expedition was over.

It seems clear that Wright made the trip with the idea in mind of extending the observations he had made in earlier trips to Cuba. It is also possible that Wright planned to stay in Santo Domingo after the departure of the Commission or to return at a later date. In one letter Wright stated, "If I were to conclude to make any considerable stay, I should expect that somebody, you or foreign botanists or our government or all would back me up strongly with moral and pecuniary support, otherwise it would be unwise for me to embark in such a labor. After a few days' examination of the vicinity of Santo Domingo City I shall be better able to decide what to do." He was encouraged by several local people to stay and continue botanical work, and he received offers of hospitality and support from residents of Santo Domingo. However, Wright's enthusiasm was dampened by the accommodations of the "Tennessee" and the attitude of the Commission. Wright, at 60 years of age, was the "oldest of all the attachés of the Commission," he wrote Gray. Nevertheless, he was regarded as a junior staff member and assigned some of the poorest quarters and mess facilities on the boat. He reported, "I have not been satisfied with my location in a mess. We are distributed among the different messes — On the back deck is the ward room mess, the middies' mess and the various forward officers' messes. With one of these I was placed while all the boys, loafers, etc., nearly are in the ward room or above . . . It was a mere accident no doubt, perhaps it was wisely ordered so, as I am better able to rough it than said boys, loafers etc." After Wright's return, Torrey referred to Wright's accommodations as the "miserable quarters — or rather filthy den that they had put him in — it being the very worst in the whole vessel," and Parry wrote that he did not think Wright "was treated as his services deserved."

From Wright's letters one also learns more of Brummel. On the first trip at Samaná, Wright reported, "At Samana the land arises abruptly into very broken hills — no mangrove swamps, no level plains, one marshy flat which might have given more of its peculiar plants had we all been waders like me. Parry didn't do much and his assistant, less, unless it be windwise and in this he can beat old Eobus. Parry came on board with a bad cold and cough which he has only now shaken off. His assistant is a gardener and is more intent (and not too much so) on gathering seeds and roots than on making specimens." Torrey, too, in later correspondence with Gray, referred to "that incompetent gardener who went with the Santo Domingo expedition."

While Wright and Parry were gathering specimens as vouchers for their observations, their activities to this end were not valued. Wright wrote Gray, "Then Wade couldn't see the use of gathering so many weeds, etc., etc. It seems to me that the Commissioners care very little for any branch of science that don't have some regard to the precious metals, coral or logwood (Mr. White has already a mahogany tree of his own on board)."

When these comments are added to those previously cited and the events which involved Parry shortly after his return, it is no wonder that the botanical results of the Commission of Inquiry were not approached with enthusiasm by the participants or their associates.

PARRY'S EXPERIENCES IMMEDIATELY AFTER THE EXPEDITION

Parry returned to his position as botanist for the U.S. Department of Agriculture in early July, 1871. On September 19th, Parry wrote to Gray of attitudes and dicta by his superior that were making his professional life difficult and his personal correspondence with Gray a violation of department rules. On September 27th he was summarily dismissed from his position. Both Torrey and Gray were incensed and decided to take action on Parry's behalf. On October 3, 1871, Gray wrote to Torrey, apparently in response to a letter from him, "Parry wrote to me about the outrageous conduct. The first thing to do is for his friends to require to know the reasons why. To write an article for the papers would only express our feeling, and do no good, perhaps harm. When you go to Washington, see Prof. Henry — you two go to the commissioner yourselves directly, and ask him what it all means — asking it in reference to scientific interests of the country as well as in justice to Dr. Parry. If there is no show of reason, — as I suppose, and the commissioner will not rectify the injustice — then go to higher authorities. If your Academy is of any good it might look into it. If things are to go on let us have the facts, and we will bring them before the scientific public, and, if deserved denounce the Agricultural bureau — as being — what Capron alone seemed to be raising it from — an institution for wasting vast sums of money." A long correspondence continued between Torrey and Gray and other American and foreign botanists concerning Parry's unwarranted discharge, and a plan of action evolved. The pertinent correspondence between Gray as spokesman for the outstanding botanists and the Commissioner of Agriculture regarding Parry's dismissal was eventually published in the *American Naturalist* (January, 1872), and the letters, as well as the opinions, were the subject of articles and editorials in other American (e.g., Am. Jour. Sci. III. 3: 315–318. 1872) and foreign scientific journals. Parry was not reinstated, however, and returned to his collecting expeditions in the West. Torrey and Gray corresponded about the possible successor to Parry, and, in a letter of November 4, 1871, Torrey expressed concern for the official attitude toward the herbarium specimens Parry had accumulated and the herbarium itself. "A new man coming in — especially if it were that incompetent gardener who went with the Santo Domingo expedition (and who Parry thinks had had much to do with his removal) might do a great deal of harm." Regarding the Santo Domingo collections Torrey wrote on January 16, 1872, "Wright ought not to let the Agric. Dept. have a set until a botanist, whom Prof. Henry and those who he may consult approve of his appointment."

The office of government botanist remained vacant until April, 1872, when George Vasey, a botanist well known to Torrey and Gray, was appointed. The fate of Parry and the feud with the Commissioner of Agriculture continued, however, for on receipt of a letter from Vasey, Gray wrote to Torrey on April 27, 1872, "I answered Vasey's letter in substance thus: 'It would give me pleasure to correspond with you personally, as I always have done though I have not time now to do so to any great extent. But as Botanist of Agriculture Depart. I meet a difficulty. I understand that you are not yourself allowed to correspond with me directly. All letters as Botanist must be signed by the Commissioner etc. Now I imagine it would not be altogether pleasant nor satisfactory for me to correspond with the commissioner etc.' — Hoisting the commissioner with his own petard? I was in some hopes that Vasey might reply that he had permission to correspond with me directly, which would have been nice." There is no further correspondence between Vasey and Gray in the historical files of the Gray Herbarium. Watts remained Commissioner of Agriculture for about ten years, and Vasey occupied the post of botanist until he died in office in 1893. Vasey apparently had learned his lesson from Parry's experience, for in his first annual report (Report of the Commissioner of Agriculture for the year 1872. Government Printing Office, 1874) Vasey states, "Deeming it an important part of the work of this division to give attention to inquiries for information on questions relating to botany, and particularly to practical and economic botany, the investigation of such questions has occupied a considerable amount of time of the present officer of the division."

In the annual reports available to me, including the historical report following Vasey's death (1894), there is no mention of the specimens of the Commission of Inquiry to Santo Domingo.

Brummel, too, had dropped from sight, with no further mention of him in the available reports of the U.S. Department of Agriculture.

DATA ON THE COLLECTIONS

There is no information available from the records of the Gray Herbarium, the Smithsonian Institution, or the U.S. Department of Agriculture to indicate when the collections of the Santo Domingo Commission of Inquiry were returned from Cambridge, nor is it clear who distributed the duplicates. These points, however, may be made with certainty:

1. The most complete set of specimens is currently in the U.S. National Herbarium.

2. The set in the Gray Herbarium, though small in number, appears to represent unicates or duplicates of specimens Wright considered to be new species or unusual records. Generally speaking, these specimens are smaller in size, truly scraps, in comparison.

3. The specimens in the Kew Herbarium were sent by Asa Gray to Oliver before the full collection was distributed. These, too, represent the new species, unusual records or questionable determinations.

4. Very few specimens have been found in the herbarium of the New York Botanical Garden.

5. A few specimens have been cited by monographers from the herbarium of the Missouri Botanical Garden. These have been checked in the families Loranthaceae, Amaryllidaceae and Vitaceae. It is possible that a larger number are there representing other families. The correspondence of Engelmann is preserved at the Missouri Botanical Garden and this has been checked. There are several letters to and from Parry indicating that Parry was notified of his position on the Commission of Inquiry several months prior to the departure of the expedition. Engelmann asked particularly that Parry collect specimens of the Cactaceae for morphological study. Engelmann was not satisfied with the results, however, for, on June 8, 1871, he wrote to Parry, "Got your different things at last. One by one. But there is confusion with me or with you. Your send. 'Cereus No. 1 smooth top.' 'wood ring' also marked No. 1. But the flowers are marked No. 2, 3. Flowers, Azua and Port au Prince all in same envelope and mixed, so which is Azua and which Port au Prince. I can not make out. Now whether No. 1 and No. 2 are the same. And Jamaica and all San Domingo seem to be beautifully mixed up. There is a living plant of a Cereus, 8 ribbed, 'flowers and notes to come.' These disjointed bits are all puzzles and rob me of a good deal of time uselessly make confusion. I am too dull to unriddle them. I shall return your notes in a few days."

A comparable complaint could have been made regarding the collections of *Agave*. In one packet mounted with an *Agave* specimen there is a note from Parry, "Capsule of Agave (I think from San Domingo) I remember it was difficult to find *mature capsules*. Do Agave like Yuccas require insect agency? In Florida the Agaves flower very freely but never perfect fruit C.C.P." The words "I think" were later crossed out. Another packet of *Agave* carries, in Parry's handwriting, the annotation "capsules and seeds from different places, San Domingo. Parry."

6. A single specimen of *Cestrum* was cited by Francey from the herbarium of the Chicago Natural History Museum.

7. The number of specimens cited by Urban and other German botanists in the various volumes of the *Symbolae Antillanae* and in *Pflanzenreich* suggest that some specimens were, or are, in the Berlin Herbarium. The collections cited are rarely those numbers sent to Oliver at Kew. Only one collection which was annotated by Urban has been seen in an American herbarium.

8. The specimens of ferns and their allies were sent to D. C. Eaton by Wright and bear Eaton's numbers. Dr. John Reeder kindly had the Eaton herbarium checked for me, and, as Series II indicates, the majority of the numbers listed in Eaton's correspondence with Wright are represented in the Yale University Herbarium. A smaller number of the fern specimens are in the National Herbarium; none has been found in the Gray Herbarium.

9. Wright must have seen the entire collection in one place at one

time. His manuscript "Flora Domingensis" contains the only reference to places, dates and numbers applicable to the entire collection.

10. No field book has been found relating to this collection. Annotations by both Wright and Gray in the manuscript refer to missing "tickets," suggesting that no field book was made.

11. The packets on some, but not all, of the herbarium sheets contain slips of paper with information on the date and location of the collections. These may be the "tickets." These slips are all in the handwriting of Charles Wright and are comparable in size and details to those commonly found with Wright's Cuban collections.

12. The numbers on the specimens and in the manuscript indicate that the collection was sorted to family and to genus before the numbering was done. Wright's manuscript indicates a number for the collection and then the location. In some cases a single number refers to a specimen in flower from one location and to another in fruit made at a different location miles away and some days later. As many as seven different collections, localities and dates are recorded to one number. This was the system employed by Asa Gray and apparently followed by Charles Wright.

13. Not all of the collections or the numbers referred to in the manuscript have been located.

14. All of the collections bear the same label of a blue-gray color stating that the specimens were distributed by the U.S. Department of Agriculture.

15. Nearly all of the sheets on which the collections are mounted are characteristically discolored, suggesting that the specimens were all poisoned at one time with bichloride of mercury. This is true of Wright, Parry, and Brummel specimens as seen in four different herbaria.

The specimens of the collection made by Wright, Parry, and Brummel as seen in American herbaria were distributed without specific dates or locations. All bear names, including unpublished epithets, as given in Wright's manuscript. A very few of the sheets have been annotated. In general, the specimens have been of questionable value for lack of appropriate data. Not even the size of the collection has been known accurately. Eaton numbered 38 collections, specimens of which are in the Yale University and the U.S. National herbaria. Not all of the species given on the list sent by Eaton to Wright have been located.

The Wright manuscript contains numbers for 634 entries. However, 26 numbers are repeated or treated as "A," "B," or "X" entries. Thirteen numbers in the numerical sequence are not used in the manuscript. Several specific entries appear for which specimens are not cited. Occasionally, locations and/or dates are given for these entries, all of which refer to cultivated plants and so may represent observations. About a dozen specimens were found in the U.S. National Herbarium with data about the specimen in the packet, while Wright's manuscript stated "without ticket" and did not cite location or date. Thirteen specimens have been located, by chance, which are not cited in the manuscript and which carry no data. The specimen of *Vaccinium meridionale* previously mentioned is such a one, as is a sterile one of "*Juniperus gracilis*" (US). These

may be all or in part from Jamaica. The total collection by Wright, Parry, and Brummel must consist of about 688 numbers.

THE LOCATIONS AND DATE OF COLLECTION

The following alphabetical listing of localities may be useful in determining the geographic location, date, and probable collector of numbered specimens. It has been compiled from the official report of the expedition, from the Wright manuscript and from locality or date slips accompanying some of the specimens seen.

1. Aguacate, *Wright*, February 13, 1871.
2. Azua, *Parry*, February 23–28, 1871.
3. Bajabonico, *Wright*, February 26–28, 1871.
4. "Deep vallies of the interior." Between Santo Domingo City and Puerto Plata, *Wright*.
5. "Interior forests." Between Santo Domingo City and Puerto Plata, *Wright*.
6. "Interior savannahs." Between Santo Domingo City and Puerto Plata, probably between El Aguacate and the Río Jima, *Wright*, February 13–15, 1871.
7. La Vega, *Wright*, February 18, 1871.
8. La Vega to Moca, *Wright*, February 18, 1871.
9. Madrigal, many from Río Jaina at Madrigal, *Wright*, February 10, 1871.
10. Moca, *Wright*, February 18–19, 1871.
11. Moca to Santiago, *Wright*, February 20, 1871.
12. Ozama River, *Wright* and/or *Parry*, February 1–8, 1871.
13. Port au Prince, collector uncertain, probably *Parry*, March 9, 1871.
14. Port Francais, *Brummel*, January 31 or February 1, 1871.
15. Puerto Plata, *Wright*, March 1–3, 1871.
16. Río Guananito, *Wright*, February 12, 1871.
17. Río Jaina, *Wright*, February 10, 1871.
18. Río Vuelta, *Wright*, February 13, 1871.
19. Samaná, *Wright & Parry*, January 24–29, 1871.
20. Santo Domingo City, *Wright* and/or *Parry*, February 1–8, 1871.
21. Santo Domingo City to Puerto Plata, *Wright*, February 9–27, 1871.
22. San Lorenzo, *Brummel*, February 1, 1871.
23. San Soreijo [San Lorenzo?], Collector unknown, locality not found.
24. Santiago, *Wright*, February 21–25, 1871.
25. Santiago to Puerto Plata, *Wright*, February 24–27, 1871.
26. Savana de la Mar, *Brummel*, February 3, 1871.

IDENTIFICATION AND PRESENT LOCATION OF THE SPECIMENS

The following lists represent enumerations of the Wright, Parry and Brummel collections made while on the Commission of Inquiry to Santo Domingo. The specimens are cited in four series. The first numerical series (I) is that compiled from the Charles Wright manuscript "Flora Domingensis" now in the archives of the Gray Herbarium. The second numerical series (II) is that reported to Charles Wright by D. C. Eaton

(letter, in the Gray Herbarium, dated October 22, 1871) and consists of ferns, lycopods and selaginellas. The numbers given were assigned by Eaton. The third series (III) is unnumbered and represents specimens which were not included in the Wright manuscript and some of which were not collected in Santo Domingo. The fourth list (IV) is alphabetical and consists of species listed by Wright, primarily as observations. These are not numbered and as far as can be determined to the present are not represented by specimens.

In each list the names preceded by an asterisk (*) were considered by Wright to represent new species. Some of these had complete descriptions in the original manuscript. There are forty-one numbers so designated which represented twenty-seven new species. If the manuscript had been published in 1872 when prepared, thirteen of the species would be recognized today, for the specimens can be assigned to acceptable species described after that date. Eight of the species are in difficult groups or consist of inadequate material and so can not be accurately assigned at the present time. Wright, Parry, and Brummel collections are the holotypes of eleven species described by other authors since 1871.

Names which are given in quotation marks in the following lists have been taken directly from the Wright manuscript and validating specimens have not been seen. Only the generic name is given if the complete epithet has not been published elsewhere. The number following the specific name refers to the alphabetical list of locations and dates given above. If such a number is not given, the Wright manuscript either listed two or more specimens, localities and dates for one collection number or the data were missing from the manuscript. The location of specimens is designated in parentheses by standard herbarium abbreviations (Lanjouw & Stafleu). The specimens as designated have either been seen by the author or are reported to occur in that herbarium and are listed in the citation of specimens by monographers and others.

Not all of the specimens listed below are satisfactorily identified. Many of the genera concerned need revision. In the difficult genera of the Loranthaceae and in the genera *Eugenia* and *Psychotria* the Wright, Parry, and Brummel specimens I have seen are of poor quality and are inadequate for determination at the present time.

Numerical Series I

1. "*Nasturtium brevipes*," 7
2. *Drymaria cordata*, 15 (US)
2B. *Sauvagesia erecta*, 6 (K, US)
3. "*Capparis cynophallophora*," 25
4. *Capparis cynophallophora* (US)
4B. *Capparis baducca* (US)
5. *Hybanthus linearifolius* (US)
6. "*Anona* sp."
6B. *Oxandra lanceolata* (US)
7. "*Bocagea laurifolia*"
8. *Polygala longicaulis*, 6 (US)
8X. *Agave intermixta*,[1] 24 (GH, MO, US)
9. *Polygala paniculata*, 15 (US)
9X. *Agave antillarum*, 24 (US)
10. *Polygala penaea*, 24 (US)
11. *Securidaca virgata*, 20 (US)
12. *Samyda dodecandra*, 20 (US)
13. *Xylosma coriaceum*, 15 (US)
14. *Xylosma coriaceum*, 15 (US)
15. *Casearia comocladia*, (US)
16. *Casearia hirsuta*, 11 (US)
17. *Casearia arborea*, 4 (US)
18. *Conocarpus erecta*, 15 (US)
19. *Conocarpus erecta* var. *sericea*, 13 (US)
20. *Combretum laxum* (US)
20X. *Ochroma pyramidale* (US)
21. *Trichilia pallida* (K, US)
22. *Xylosma coriaceum*, 15 (US)
23. *Rhacoma crossopetalum*, 15 (US)
23B. *Schafferia frutescens*, 15 (US)
24. *Rhacoma ilicifolia*, 6 (US)
25. *Begonia brachypoda*, 25 (US)
26. *Melothria guadalupensis* (K, US)
27. *Passiflora suberosa* (US)
28. "*Passiflora pallida*"
29. *Passiflora murucuja*, 19 (F, MO, US)
30. *Passiflora suberosa* (US)
31. *Anguira pedata* (US)
32. *Cayaponia racemosa* (US)
33. *Sechium edule* (US)
34. *Mormordica charantia* (US)
35. *Fevillea cordifolia* (US)
36. "*Turnera ulmifolia*"
36. "*Phaseolus clitorioides*," 19
37. "*Piriqueta cistoides*," 6
38. "*Malachra texana*," 15
39. *Sida acuminata* (K, US)
40. *Sida hederaefolia* (US)
41. *Dalechampia scandens*, 2 (US)
41. **Rhacoma gonoclada*,[2] 20 (K)
42. *Wissadula amplissima*, 20 (US)

[1] Trelease studied the Wright, Parry, and Brummel material of *Agave*, noting that it was a mixed collection (**Mem. Natl. Acad. Sci. 11:** 31, 32, *pls. 41–43, 64.* 1913). Part of the collection was referred to *Agave antillarum* Descourt. and part was selected as the type of *Agave intermixta* Trelease. (Trelease had prepared a complete description of this species and a discussion of its affinities. Such a manuscript is currently in the herbarium of the Missouri Botanical Garden. For some unknown reason a much abbreviated description was given as a footnote in the reference cited above and the discussion was never published.) The single specimen in the Gray Herbarium is without number, but in a packet is a field note carrying most of the data given in the Wright manuscript. The same slip indicates that a specimen was sent to Dr. Engelmann and it is this specimen at the Missouri Botanical Garden which was designated as the holotype by Trelease. The collection was made on the bank of a stream near Santiago de los Caballeros on February 22, according to the field notes. In the manuscript Wright stated the collection was made on "steep hills" near Santiago.

The text for *Plate 43* in Trelease's monograph of the genus *Agave* in the West Indies suggests that the leaf margin included in *Figure 1* may be that of *Agave intermixta*. This illustration agrees with the leaf specimen in the Gray Herbarium which is mounted on the same sheet with the flowers typical of *Agave intermixta* and not *Agave antillarum*.

[2] Wright used the name "*Myginda gonioclada*, n. sp.," in his manuscript. Kuntze cited this name in synonymy when transferring the species to the genus *Crossopetalum* (Rev. Gen. **1**: 116. 1891). Kuntze does not indicate where he saw the name Wright

43. *Malvastrum spicatum*, 20 (US)
44. *"Malachra capitata,"* 19
45. *Centrosema virginiana*, 19 (US)
45. *"Melochia tomentosa"*
46. *Sida ciliaris* (US)
47. *Sida rhombifolia*, 21 (US)
48. *Pithecellobium circinale*, 2 (GH, US)
49. *Bauhinia divaricata*, 13 (US)
50. *Acacia tortuosa* (US)
51. **Rhacoma gonoclada*, 2 (K, US)
52. *Caesalpinia pauciflora*, 13 (US)
53. *Corynella dubia*, 13 (GH, US)
54. *Rhodopis planisiliqua* (GH, US)
54. *Guarea trichiloides*, 21 (US)
55. blank
56. blank
57. **Vilmorinia glyciphylla*, 21 (GH, US)
58. *Calliandra portoricensis*, 20 (US)
59. *"Desmodium incanum,"* 19
60. *Calopogonium caeruleum*, 20 (US)
60. *"Mimosa ceratonia"*
61. *Acacia lutea*, 20 (GH, US)
62. *Centrosema pubescens* (US)
63. *"Galactia cubensis,"* 19
64. *"Aeschynomene sensitiva,"* 19
65. *"Vigna luteola,"* 19
66. *"Mimosa ceratonia"*
67. *Phaseolus adenanthera*, 19 (US)
68. **Inga vera*, 19 (K)
69. *Acacia lutea* (US)
70. *Crotalaria retusa*, 19 (US)
71. *Mucuna sloanei* (US)
72. *"Rhynchosia reticulata"*
73. *Cassia biflora*, 20 (GH, US)
74. *Albizia lebbeck* (US)
75. *Inga laurina*, 15 (US)
76. **Poitea galegoides*, 21 (US)
77. *Stylosanthes hamata*, 20 (US)
78. *Sophora tomentosa* (US)
79. *"Cassia diphylla"*
80. **Vilmorinia glyciphylla*, 21 (K)
81. *Desmanthus virgatus* (US)
81B. *"Anguria pedata"*
82. *Crotalaria verrucosa*, 15 (GH, US)
83. *Senegalia angustifolia*, 25 (US)
84. *Teramnus uncinatus* (US)
85. *Desmanthus virgatus* (US)
86. *Inga laurina* (US)
87. **Vilmorinia glyciphylla*, 21 (US)
88. **Corynella paucifolia*, 9 (K, US)
89. *Barbieria pinnata*, 21 (US)
90. *"Mimosa ceratonia,"* 21
91. *Poitea galegoides*, 21 (US)
92. *Alysicarpus nummularifolius* (US)
93. *Poitea galegoides*, 21 (US)
94. *Desmodium adscendens*, 9 (US)
95. *Erythrina poeppigiana*, 9 (US)
96. *Pictetia spinifolia* var. *ternata*, 24 (US)
97. **Corynella paucifolia*, 24 (K, GH)
98. *Ateleia gummifera*, 24 (US)
99. *Poiretea scandens*, 21 (GH, US)
100. *Haematoxylon campechianum*, 20 (GH, US)
101. blank
102. *Hibiscus brasiliensis* (US)
103. *Pavonia spinifex*, 20 (US)
104. *Sida acuta* (US)
105. *Melochia nodiflora*, 19 (US)
105. *Sida rhombifolia*, 19 (US)
106. *Corchorus hirsutus* (US)
106A. *"Urena sinuata"*
107. *Helicteres jamaicensis* (US)
108. *Melochia tomentosa*, 13 (US)
109. *"Corchorus hirtus,"* 21
110. *Waltheria americana*, 20 (US)
111. *Triumfetta lappulacea*, 19 (K, US)
111A. *"Triumfetta semitriloba"*
112. *Malpighia domingensis*, 24 (US)
113. *Stigmaphyllum lingulatum*, 24 (US)
114. *Stigmaphyllum ovatum*, 19 (US)
114A. *"Cordia laevigata"*
115. *Stigmaphyllum ovatum*, 19 (US)

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coined. Oliver, in correspondence, reported Wright's new species to be similar to another specimen collected by Schomburgk at Azua. Urban finally described *Rhacoma gonoclada* (Symb. Ant. **5**: 75. 1904). He cited both the names used by Wright and Kuntze and indicated that he saw the specimen in the Kew Herbarium. The number "41" here duplicated from Wright's manuscript is probably an error for "51."

116. *Bourreria succulenta* (US)
117. *Byrsonima coriacea*, 1 (US)
118. *Bunchosia media*, 7 (US)
119. *Stigmaphyllum lingulatum*, 20 (US)
120. *Stigmaphyllum lingulatum*, 15 (US)
121. *Malpighia domingensis*[3] (US)
122. *Stigmaphyllum angulosum*, 20 (US)
123. *Triopteris ovata*, 13 (GH, US)
124. *Malpighia aquifolia*, 2 (US)
125. *Malpighia domingensis*, 20 (US)
126. *Thryallis glauca*, 20 (US)
127. *"Triopteris rigida,"* 15
128. *Banara domingensis* (K, US)
129. *"Guarea trichilioides,"* 19
130. *Picramnia pentandra* (US)
131. *Corchorus siliquosus* (US)
132. *Melochia pyramidata* (US)
133. *Colubrina ferruginosa*, 20 (US)
134. *Muntingia calabura* (US)
135. *Hydrocotyle hirsuta*, 20 (US)
136. *Dalbergia ecastophyllum*, 19 (US)
137. *Rondeletia berteriana*, 20 (GH, US)
138. *"Picramnia pentandra"*
139. *"*"*Myrtus* (*Eugenia*) sp. nov.,"[4] 20
140. *Miconia racemosa*, 21 (US)
141. *"Miconia laevigata,"* 19
142. *Clidemia hirta*, 19 (US)
143. *Miconia prasina*, 19 (US)
144. *Ossaea acuminata*, 2 (US)
145. *"Miconia nicotianafolia,"* 2
146. *Acidanthera quadrata*, 6 (US)
147. *Miconia racemosa*, 21 (US)
148. *Nepsera aquatica*, 6 (US)
149. *Miconia laevigata*, 19 (US)
149A. *"Nepsera aquatica,"* 6
150. *Miconia prasina*, 26 (US)
151. *"Miconia impetiolaris,"* 19
151A. *"Casearia ilicifolia"*
152. *Picramnia pentandra* (US)
153. **Serjania polyphylla* (US)
154. *Paullinia pinnata*, 19 (US)
155. *Gouania lupuloides*, 19 (US)
156. *Gouania polygama*, 19 (US)
157. *Serjania polyphylla*, 19 (US)
158. *Rajania cordata* (US)
159. **Serjania sinuata*,[5] 25
160. *Securidaca virgata*, 19 (US)
161. *Allophylus rigidus*, 13 (US)
162. *Rourea surinamensis*, 21 (US)
163. *Eugenia pseudopsidium* var. *portoricensis*,[6] 20 (US)
164. *Mouriria domingensis*, 10 (US)
165. *Syzygium jambos* (US)
166. *Eugenia* aff. *umbellulifera*, 20 (US)
167. *Eugenia monticola* (US)
168. *Eugenia myrtoides*, 15 (US)
169. **Eugenia* sp. nov. (K)
170. **Eugenia* sp. nov.[7] (GH, US)

[3] Small selected this specimen as the holotype of *Malpighia domingensis* (N. Am. Fl. **25**: 156. 1910). According to the Wright manuscript, the specimen was collected on February 14, 1871, when Wright was in the area between Río Maimon and Hato del Banao. Collections *112* and *125* listed by Wright as the same were made at Santiago and Santo Domingo City respectively.

[4] Wright described this collection, citing also No. 166, as a new species. He reported "collected from bushes 10–15′ growing nearly on the site of the old city of SD hence it is as likely to be something introduced from abroad as to be indigenous. Feb. 30. The species seems most likely to belong to Berg's genus Myrcianthus or possibly to Myrtus." The date given is in error but no correction can be offered. Wright was in Puerto Plata on February 30th and he did not arrive in Santo Domingo City until January 31st in the earlier part of his trip.

[5] This collection was named *"Serjania apiculata* n. sp." by Wright. On the field label Wright reported the collecting locality to be between Santiago and Puerto Plata and the date, February 25. Radlkofer (Pflanzenr. IV. **165**(Heft 98a): 117. 1933) gave Wright's unpublished name and reported he saw a specimen in the Kew herbarium.

[6] This specimen bears the annotation, "determined by Urban."

[7] The collections *169* and *170* are cited in the Wright manuscript as new species with an unpublished name. Collection *169* was sent to Oliver at Kew. Both collections were made on February 18th and on that date Wright was between Santo

171. *Ternstroemia peduncularis*, 21 (US)
172. *Ardisia escallonioides*,[8] (GH, K, US)
173. *"Prunus sphaerocarpa,"* 25
174. *Simaruba glauca*, 9 (US)
175. *Sesuvium portulacastrum* (US)
176. *Hydrocotyle umbellata*, 19 (US)
177. *Bourreria virgata* (US)
178. *Hirtella triandra*, 19 (US)
179. *Guaiacum officinale*, 2 (US)
180. *Lawsonia inermis* (US)
181. *Jussiaea leptocarpa*, 19 (K, US)
182. *Jussiaea leptocarpa*, 19 (US)
182A. *"Jussiaea salicifolia"*
183. *Jussiaea erecta*, 19 (US)
184. *Cissus caustica*, 8 (US)
185. *Ampelocissus robinsonii* (GH, K, MO, US)
186. *"Vitis sicyoides,"* 19
187. *Bursera simaruba*, 19 (US)
188. *Anacardium occidentale* (US)
189. **Comocladia dentata* (GH, K, US)
190. **Comocladia domingensis*[9] (US)
191. *Comocladia dodonaea*, 20 (US)
192. **Comocladia cuneata*[10] (K, US)
193. *Calophyllum brasiliensis* var. *antillanum*, 19 (US)
194. *Chrysobalanus icaco*, 23 (US)
195. *Eugenia pseudopsidium* var. *portoricensis*, 20 (US)
196. *Comocladia dodonaea*, 20 (GH, US)
197. *Tetragastris balsaminifera*, 9 (K, US)
198. *"Lagenaria vulgaris,"* 24
199. *Annona reticulata* (US)
200. *Mormordica charantia* (US)
201. *Chrysophyllum olivaeforme*, 20 (US)
201. *Centrosema virginiana* (US)
202. *Chrysophyllum argenteum*, 9 (US)
203. **Chrysophyllum olivaeforme* (K, GH)
204. **Psychotria pinularis*, 15 (US)
205. *Psychotria tenuifolia* (US)
206. *Psychotria domingensis*, 19 (US)
207. *Psychotria grandis*, 19 (US)
208. *"Psychotria uliginosa,"* 19
209. *Psychotria berteriana* (GH, US)
210. *Palicourea barbinervia* (US)
211. *Psychotria brachiata*, 21 (US)
212. *Hamelia patens*, 19 (US)
213. *Palicourea domingensis* (US)
214. *Chiococca alba* (US)
215. *"Ernodea litoralis,"* 15
216. *"Ixorea ferrea,"* 15
217. *Psychotria revoluta*, 15 (US)
218. *Micromeria viminea*, 13 (US)
219. *"Rauwolfia nitida,"* 20
220. *Ernodea litoralis*, 15 (US)
221. *Diodia maritima*, 15 (US)
222. *Cornutia pyramidata*, 15 (US)
223. *Borreria ocimoides* (US)
224. *Bourreria domingensis*, 20 (US)
225. *Guettarda scabra* (US)
226. *Chione exserta*, 9 (GH)
227. *Psychotria revoluta*, 9 (US)
228. *Borreria verticillata*, 17 (US)
229. *"Borreria parviflora,"* 9
230. *Manettia calycosa*, 21 (US)
231. *Borreria ocimoides* (US)

Cerro and Moca. The two specimens of *170* which I have seen can not be identified with certainty at this time.

[8] This collection was identified and cited by Mez (Pflanzenr. IV. **236**(Heft 9): 81. 1902) who apparently saw the specimen at Kew. Urban (Symb. Ant. **8**: 520. 1921) and Moscoso (Cat. Flor. Dom. 471, 1943) repeated the reference. Wright's manuscript noted that "no ticket" was available to give location and date of the collection.

[9] The Wright manuscript notes that this collection has a "mixed ticket." The locality given is Santo Domingo City but the data apply to a species of *Piper*. Britton selected this collection as the type of his new species (Bull. Torrey Club 37: 350. 1910).

[10] Britton selected the specimen at the U.S. National Herbarium as the type of his new species *Comocladia acuminata* (Bull. Torrey Club 37: 349. 1910). Since this epithet is a later homonym, he renamed it *Comocladia cuneata* (Bull. Torrey Club **41**: 9. 1914). Wright's manuscript reported the collection was without data.

232. *Borreria laevis*, 9 (US)
233. *Erithallis vaccinaefolia*, 9 (US)
234. *Randia aculeata* (GH, K)
235. *Antirrhoea lucida*, 25 (US)
236. *Parathesis serrulata*, 19 (US)
237. **Guettarda preneloupii*[11] (K, US)
238. *Guettarda scabra*, 21 (US)
239. *Sauvagesia erecta*, 21 (US)
239. *Tournefortia scabra*, 21 (US)
240. *Tournefortia scabra*, 21 (US)
240. *Diodia sarmentosa* (US)
241. **Randia erythrocarpa*, 13 (US)
242. *Catesbaea parvifolia*, 2 (US)
243. *"Ixorea ferrea,"* 15
244. *Psychotria brachiata*, 21 (US)
245. *Erithallis fruticosa* (K)
246. *Randia parvifolia* (US)
247. *Eupatorium* sp.,[12] 13 (US)
248. ***Gochnatia oligantha*** (Urban) Howard, comb. nov.[13] (GH, K)
249. *Enhydra sessilis*, 19 (US)
250. blank
251. *Eleutheranthera ruderalis*, 7 (US)
252. *Eupatorium odoratum*, 20 (US)
253. *Mikania scandens*, 19 (US)
254. *Mikania cordifolia*, 19 (US)
254. *Luffa cylindrica* (US)
255. *Salmea scandens*, 19 (US)
256. *"Wedelia carnosa,"* 19
257. *Pacourina edulis*, 19 (GH, US)
258. *Borrichia arborescens* (US)
259. *Melanthera Buchii* 19 (US)
260. *Erigeron jamaicensis* (US)
261. **Chaptalia primulacea*,[14] 15 (GH, K)
262. *Pluchea odorata* (US)
263. *Porophyllum ellipticum* (US)
264. *Ageratum conyzoides* (US)
265. *Eupatorium obtusissimum* (US)
266. *Verbesina alata* (US)
267. *Tithonia rotundifolia* (US)
268. **Senecio haitiensis*, 25 (K, US)
269. *Chaptalia nutans*, 6 (US)
270. *Vernonia racemosa*, 11 (US)
271. *Senecio plumbeus*, 15 (US)
272. *Erigeron jamaicensis*, 10 (US)
273. *Vernonia sprengeliana*, 20 (US)
274. *Vernonia sprengeliana*, 20 (US)
275. *Eupatorium obtusissimum*, 15 (US)
276. *Synedrella nodiflora*, 19 (US)
277. *Salmea scandens*, 19 (US)
278. *Wedelia gracilis*, 21 (US)
279. *Vernonia buxifolia*, 21 (US)

[11] Wright's manuscript gives two dates, February 3 and 9, for this collection made between Santo Domingo City and Puerto Plata. On both dates Wright was in the vicinity of Santo Domingo City.

[12] Wright used an unpublished specific name (referring to the incised margin of the leaves) which he attributed to Grisebach. I have been unable to identify accurately the material cited.

[13] Urban described this as *Anastraphia oligantha* (Symb. Ant. **3**: 417. 1903), the basionym of the new combination above, citing in synonymy *Anastraphia pauciflosculа* used by Wright in his manuscript and on the specimens of this number. Wright's invalid name was also used by Hitchcock (Ann. Rep. Mo. Bot. Gard. **4**: 102. 1893). Urban cited only a collection by Wright, Parry, and Brummel, without giving it a number. In a later publication (*loc. cit.* **8**: 746. 1921) Urban refers to "Wright, Parry and Brummel 248." This collection must be considered the type, and, although Urban does not indicate the source of his material, he must have examined the specimen at Kew which is to be considered the holotype. Roy Jervis has annotated the specimen in the Gray Herbarium with a name transferring the species to the genus *Gochnatia*. This combination was not published. Wright indicated in his manuscript that the field label with location and date are missing.

[14] Wright annotated this collection with an unpublished name referring to the long leaves. He sent a specimen to Oliver who suggested it had affinities with *Chaptalia longiflora*. Greene described the collection as *Chaptalia primulacea* (Leafl. Bot. Obs. **1**: 195. 1906) selecting a specimen in the U.S. National Herbarium as the holotype. Robinson annotated both the Gray Herbarium specimen and the Greene publication suggesting that the species is the same as *Chaptalia membranacea* Urban. The collection was made on March 2, at Puerto Plata.

280. *Pectis carthusianorum*, 6 (US)
281. *"Chrysanthellum procumbens,"* 10
282. *Pectis procumbens*, 6 (US)
282. *Hieracium gronovii* (GH)
283. blank
284. **Isodorea pungens*,[15] 20 (GH, K, US)
285. *Wallenia laurifolia*, 19 (US)
286. *Wallenia laurifolia*, 19 (US)
287. *Erithallis fruticosa*, 19 (US)
288. *Randia aculeata* (US)
289. *Gonzalagunia spicata*, 19 (US)
290. *Chiococca alba*, 19 (US)
291. *Psychotria revoluta* (US)
292. *"Palicourea guianensis"*
292. *Palicourea crocea*, 19 (US)
293. *Palicourea barbinerve* (US)
294. *Palicourea riparia*, 19 (US)
294B. *Palicourea crocea* (US)
295. *"Psychotria berteriana,"* 19
296. *Psychotria pubescens*, 19 (US)
297. **"Psychotria* sp. nov.,"[16] 9 (GH)
297. *Psychotria microdon*, 15 (US)
298. *Diodia rigida*, 6 (US)
299. *Spermacoce tenuior*, 15 (US)
300. *"Spermacoce* sp.,"[17] 19
301. **Lobelia salicina*, 19 (K, US)
302. *Lobelia cliffortiana*, 20 (US)
303. *"Conradia reticulata,"* 4
304. *"Ardisia crenulata,"* 19
305. *Dipholis salicifolia*, 19 (US)
306. *"Jacquinia ruscifolia,"* 24
307. *Citharexylum fruticosum* (US)
308. *Jacquinia Eggersii* (US)
308. *Citharexylum fruticosum* (US)
309. *Hippocratea volubilis* (US)
310. *Cestrum macrophyllum*, 19 (US)
311. *Solanum polyacanthum*, 21 (US)
312. *"Solanum callicarpaefolium"*
313. *Cestrum diurnum*[18] (F)
314. *"Cordia globosa"*
315. *Bourreria virgata*, 24 (US)
316. *Cordia curassavica* (US)
317. *"Nama jamaicensis"*
318. *Buchnera elongata*, 6 (US)
319. *Cordia lima*, 7 (US)
320. *"Melochia serrata"*
321. *Cordia serrata*, 13 (US)
322. *Cordia sebestena* (K, US)
323. *Wigandia urens*, 16 (US)
324. *Cordia nitida* (US)
325. *"Pavonia typhalea"*
326. *Scoparia dulcis*, 20 (US)
327. blank
328. *"Bourreria virgata,"* 24
329. *Cordia globosa* (US)
330. *Lantana involucrata*, 15 (US)
331. *"Capraria biflora"*
332. *Bacopa stricta*, 21 (GH, US)
333. *Gerardia fasciculata*, 6 (US)
334. *Lobelia domingensis*, 6 (K, US)
335. *Ammania latifolia*, 21 (US)
336. *Cordia sulcata*, 19 (GH, US)
337. *Lantana camara* var. *mista*,[19] 19
338. *"Heliotropium parviflorum,"* 20
339. blank
340. *"Scutellaria havanensis,"* 19
341. *Ocimum gratissimum* (US)
342. *Leonotis nepetaefolia*, 19 (US)
343. *Hyptis pectinata*, 19 (US)
344. *Scutellaria havanensis*, 15 (US)

[15] In his manuscript Wright recognized this collection as a "new species" which he called *Isodorea pungens* citing in synonymy *Ernodea pungens* Lam. Robinson had access to the Wright manuscript and the specimen in the Gray Herbarium, although he neither cited the specimen nor gave Wright credit in making the new combination *Isodorea pungens* (Lam.) Robinson (Proc. Amer. Acad. Arts Sci. **45**: 401. 1910). Wright's specimen was collected on cliffs by the river, near Santo Domingo City, on February 3.

[16] This material is inadequate for accurate determination but appears to be *Psychotria pinularis*.

[17] The Wright manuscript ascribes a specific name attributed to Jacquin to this collection. I can find no reference to the publication of this epithet.

[18] Wright's manuscript cites *"Solanum verbascifolium"* for this number; however, Francey in his monograph of *Cestrum* (Candollea **6**: 286. 1936) cites a specimen from the Chicago Natural History Museum as given above.

[19] This collection, as well as *357*, was cited by Moldenke (An alphabetized list of citations **3**: 1146. 1949) as identified. The herbarium source of the material is not stated.

345. blank
346. *Hyptis suaveolens*, 19 (US)
347. *Hyptis capitata*, 19 (US)
348. *Hyptis lantanifolia*, 9 (US)
349. *Ocimum gratissimum*, 19 (US)
350. *"Salvia occidentalis"*
351. *Hyptis americana*, 19 (US)
352. *Hyptis pectinata*, 19 (US)
353. *Stachytarpheta jamaicensis*, 19 (GH, US)
354. *Priva lappulacea*, 20 (US)
355. *Petitia domingensis*, 7 (US)
356. *Clerodendron aculeatum* (US)
357. *"Cornutia pyramidata,"* 15
358. *Acalypha alopecuroides* (US)
359. *Acalypha setosa*, 20 (GH, US)
360. *Blechum brownei* (US)
361. *Dicliptera assurgens*, 20 (US)
362. *Ruellia tuberosa* (US)
363. *Teliostachya alopecuroides*, 9 (US)
364. *Barleriola solanifolia*, 2 (US)
365. **Ruellia coccinea*, 19 (K, US)
366. *Justicia pectoralis* (US)
367. *Justicia sessilis*, 20 (US)
368. *Ruellia domingensis*, 21 (US)
369. *Justicia pectoralis*, 19 (GH, US)
370. *Cordia serrata*, 21 (US)
371. *Jacquemontia pentantha*, 20 (US)
372. *Jacquemontia nodiflora* (US)
373. *Merremia umbellata*, 20 (US)
374. *"Ipomoea umbellata,"* 20
375. *Rivea corymbosa*, 20 (US)
376. *Merremia quinquefolia* (US)
377. *Jacquemontia nodiflora* (US)
378. *Ipomoea eriosperma* (US)
379. blank
380. *"Ipomoea campanulata,"* 19
381. *"Ipomoea cathartica"*
382. *"Ipomoea fastigiata"*
383. *"Ipomoea cathartica"*
384. *Ipomoea acuminata* (US)
385. *Ipomoea acuminata* (US)
386. *"Ipomoea fastigata"*
387. **Ipomoea setifera*,[20] 19 (GH, K)
388. *Ipomoea tiliacea* (US)
389. *Ipomoea tiliacea* (US)
390. *Rivea campanulata*, 19 (US)
391. *Cuscuta americana*, 20 (US)
392. *"Limnanthemum humboldtianum,"* 10
393. *Schultesia heterophylla*, 6 (US)
394. *Micranthemum nuttallii*, 18 (US)
394B. **"Micranthemum* sp. nov.,"[21] (GH, K)
395. *"Utricularia pusilla"*
395. *Tabernaemontana citrifolia*, 6 (US)
396. *"Tabernaemontana neriifolia"*
396. *Psychotria undata* (GH, US)
397. *"Ipomoea fastigiata"*
397. *Rhabdadenia berterii*, 21 (US)
398. *"Tabernaemontana neriifolia,"* 15
399. *Distictis lactiflora* (K)
400. *Calatropis procera* (US)
401. *Isotoma longiflora*, 19 (US)
402. *Rhabdadenia paludosa*, 19 (US)
403. *Asclepias nivea* (US)
404. *"Echites umbellata"*
405. *Echites umbellata* (US)
406. *Urechites lutea*, 15 (US)
407. *Rauvolfia nitida*, 20 (US)
408. *Anagadenia berterii*, 21 (US)
409. *"Echites repens,"* 19
410. *Exostema longiflorum* (US)
411. *"Metastelma leptocladon,"* 21
412. *"Piper dilatatum,"* 21
412. *Metastelma Picardae* (US)
413. *Tabernaemontana amygdalifolia*, 17 (US)
414. *"Cestrum pallidum,"* 20
415. *Nectandra antillana*, 9 (US)
416. *"Phoebe montana,"* 21
417. blank
418. *Linociera domingensis*, 21 (US)
419. *"Nectandra willdenoviana"*
420. *Ocotea leucoxylon*, 19 (US)
421. *"Nectandra willdenoviana"*

[20] This collection bears an unpublished specific name relating to the peninsula of Samaná where the specimen was collected January 27, 1871. Neither this specimen nor any of the other Convolvulaceae here have been cited by House or other monographers of the family.

[21] Wright had prepared a complete description for publication but was unable to supply data on the date or location of the collection. The genus requires a monographic treatment before the cited specimens can be determined.

422. *Licaria triandra*, 10 (US)
423. *Trichostigma octandrum*, 21 (US)
424. *"Pisonia aculeata,"* 9
425. *Pisonia aculeata*, 25 (US)
426. *Rapanea guianensis* (US)
427. *Rapanea ferruginea*, 9 (GH, US)
428. *"Chamissoa altissima,"* 20
429. *Iresine angustifolia*, 20 (US)
430. *Alternanthera geniculata* (US)
431. *"Rousselia lappulacea,"* 19
432. *Pilea repens*, 19 (US)
433. *Fleurya aestuans* (US)
434. *Urera baccifera*, 19 (US)
435. *Ficus trigonata*, 8 (US)
436. *Ficus citrifolia*, 8 (US)
437. *Ficus citrifolia*, 8 (US)
438. *Ficus trigonata*, 10 (US)
439. *"Marcgravia umbellata"*
440. *Piper aduncum*, 19 (US)
441. *Piper aduncum*, 19 (US)
442. *Piper dilatatum* (US)
443. *Piper jacquemontanum*,[22] 19 (GH, US)
444. *Piper marginatum*, 21 (MO, US)
445. *Piper hispaniolae* [23] (US)
446. *Piper parryanum*,[24] 19 (US)
447. *Piper dilatatum* (US)
448. *Piper parryanum*, 19 (GH, MO, US)
449. *Peperomia distachya*, 19 (US)
450. *"Peperomia caulibarbis"*
451. *Peperomia serpens*, 19 (US)
452. *Peperomia serpens*,[25] 19
453. *Peperomia glabella*, 19 (US)
454. *Dendrophthora marmeladensis*, 21 (US)
455. *Dendrophthora marmeladensis*, 21 (US)
456. *"Dendrophthora wrightii,"* 21
457. *Dendrophthora flagelliformis*, 15 (US)
458. *Phoradendron anceps*, 15 (US)
459. **Phoradendron cerinocarpum*
459A. *Phoradendron chrysocarpum* [26] (US)
460. *Phoradendron hexastichum*, 21 (US)
461. **Phoradendron mucronatum* (GH, K, US)
462. *Phoradendron mucronatum*, 9 (US)
463. *Dendrophthora flagelliformis*, 15 (US)
464. *Phoradendron dichotomum*, 10 (US)
465. *Phoradendron piperoides*,[27] 25 (US)
466. *Phoradendron dichotomum*, 24 (US)
467. *Phoradendron antillarum*, 21 (US)
468. *Dendropemon purpureus* (US)
468A. *Dendropemon uniflorus* (US)
469. **Dendropemon alatus* (GH, K, US)
470. **Dendropemon alatus*, 2 (GH, K, US)

[23] This collection was cited by Trelease (Repert. Sp. Nov. **23:** 307. 1927) as given above.

[23] Trelease selected the specimen in the U.S. National Herbarium as the holotype of this species which he described as new (*loc. cit.* 309). Wright's manuscript gives one collection number but two locations for the material: Puerto Plata, February 26, and Samaná, January 27. I have been unable to determine the original locality of the holotype.

[24] Trelease cited *Wright, Parry & Brummel 446* and *448* in describing this species as new (*loc. cit.* 311). Number *446* was selected as the holotype in the U.S. National Herbarium. Both collections were made in Samaná on January 28, 1871.

[25] Trelease (*loc. cit.* 323) cited this collection number without indicating the location of the specimen.

[26] *Wright, Parry & Brummel 459* is cited by Trelease (The Genus *Phoradendron*. Univ. Ill. Bull. **13:** 139. 1916) as the holotype of *Phoradendron cerinocarpum*. The specific epithet is attributed to Wright and occurs in the manuscript. Unfortunately, the numerical designation in the Loranthaceae is badly mixed. Number *459* is reported to have been collected between Moca and Santiago, on February 21, and on the road from Santo Domingo City to Puerto Plata, on February 13, a date when Wright was in the vicinity of Loma Laguneta and El Aguacate.

[27] Cited under this name by Trelease (*loc. cit.* 147).

471. *Suriana maritima*, 13 (US)
472. *Coccoloba swartzii*, 21 (GH, K, US)
473. *Coccoloba swartzii*, 21 (GH, US)
474. **Coccoloba fuertesii*, 21 (GH, K, US)
475. **Coccoloba nodosa*, 21 (GH, K, NY, US)
476. **Coccoloba incrassata*, 2 (GH, K, US)
477. **Coccoloba diversifolia* (GH, US)
478. *Exostema caribaeum*, 2 (US)
479. *Pisonia aculeata* (US)
480. *Cyathula achryanthoides*, 19 (US)
481. *Fleurya aestuans*, 21 (US)
482. *Pilea repens*, 17 (US)
483. *Rousselia humilis*, 19 (US)
484. *Tabebuia berteri*, 6 (US)
485. *Tabebuia berteri* (US)
486. *Forsteronia corymbosa* (US)
487. *Rhabdadenia paludosa* (US)
488. "*Echites repens*," 19
489. *"*Guettarda* sp. nov." [28]
490. *Jatropha gossypifolia* (US)
491. *Adelia ricinella*, 2 (US)
492. *Acalypha setosa*, 19 (GH)
493. *Acalypha glechomifolia* (US)
494. *Clerodendron aculeatum* (US)
495. *Argithamnia candicans*, 15 (US)
496. "*Phyllanthus nobilis*," 25
497. "*Drypetes alba*," 19
497. *Psychotria revoluta*, 19 (K, US)
498. *Drypetes alba* (US)
499. "*Drypetes* sp. nov.," [29] 15
500. *Drypetes alba*, 15 (US)
501. *Drypetes alba*, 21 (US)
502. **Ilex* aff. *macfadyenii*,[30] 21 (US)
503. *Croton origanifolius* (GH, US)
504. "*Croton flavens*," 2
505. *Croton pallidus* (GH)
506. *Croton discolor*, 24 (US)
507. *Croton linearis*, 13 (US)
508. *Euphorbia prostrata* (US)
509. *Euphorbia buxifolia*, 13 (US)
510. "*Euphorbia heterophylla*," 15
511. *Euphorbia hirta*, 19 (US)
512. *Euphorbia heterophylla*, 15 (US)
513. *Solanum antillarum*, 21 (US)
514. *Peperomia obtusifolia*,[31] 9 (US)
515. *Erithallis fruticosa*, 15 (K, US)
516. *Stigmaphyllon lingulatum* (US)
517. *Exothea paniculata*, 19 (US)
518. **Cuphea micrantha* [32] (K)
519. *Cuphea parsonsia*, 16 (US)
520. "*Miconia fothergilla*," 9
521. *Miconia macrophylla*, 1 (US)
522. *Tetrazygia bicolor*, 6 (US)
523. *Heterotrichum umbellatum*, 21 (US)
524. *Ossaea acuminata*, 6 (US)
525. *Miconia elata*, 21 (US)
526. *Miconia rubiginosa*, 9 (GH, US)
527. *Dieffenbachia seguine*, 19 (US)
528. *Costus cylindricus*, 19 (GH, US)
529. *Pistia stratiotes*, 7 (US)
530. *Hypoxis erecta*, 6 (US)
531. *Heteranthera limosa*, 6 (US)
531A. *Heteranthera spicata* (US)
532. *Cipura palludosa*, 6 (US)
533. *Anthurium scandens*, 4 (US)
534. *Tillandsia valenzuelana* (US)
535. "*Anthurium* sp.," [33] 19
536. "*Anthurium* sp.," [33] 19
537. *Cissampelos pareira* (US)

[28] No material has been seen of this number. Wright described a new species in his manuscript citing *237* and *489*. The former has been referred to *Guettarda preneloupii*. The collections were made near Santo Domingo City on February 3rd and 9th.

[29] Wright compared his material with "*Drypetes incurva* Mull." and suggested it was perhaps a distinct species. The specimen was collected at Puerto Plata on February 26. No material has been located.

[30] Wright's notes indicate that he collected this specimen on February 15 when he travelled in the vicinity of the Arroyo Yuma, the Río Yuna and the Río Jima.

[31] Trelease had annotated this sheet with a new specific name honoring Brummel and indicated this as the type. The name apparently was never published.

[32] This specimen has not been cited by monographers of the Lythraceae. The unpublished specific name referred to Santo Domingo. The specimen was collected "in the savannas of the interior at Madrigal" on February 11, 1871.

[33] Wright uses in his manuscript a name attributed to Schott which appears to be unpublished. No description is given and no specimens have been located.

538. *Dioscorea polygonoides*, 19 (US)
539. *Smilax populnea*, 15 (US)
540. *Smilax domingensis* (US)
541. *Callisia monandra*, 20 (US)
542. *Tradescantia geniculata* (US)
543. *Commelina elegans*, 19 (GH, US)
544. *Commelina elegans* (US)
545. *Commelina diffusa*, 20 (US)
546. *Callisia monandra*, 21 (US)
547. *Thrinax parviflora*, 20 (US)
548. blank
549. *Coccothrinax* sp.,[34] 14 (US)
550. *Copernicia* sp.,[34] 2 (US)
551. *Pleurothallis gelida*, 5 (US)
552. *Epidendrum rigidum*, 19 (US)
553. "*Aeranthus* sp.," 9
554. *Tetramicra parviflora* (GH, US)
555. blank
556. *Ponthieva glandulosa*, 5 (US)
557. "*Spiranthes elata*," 21
557A. *Pelexia* sp. (US)
558. "*Pelexia setacea*"
559. *Malaxis spicata*, 19 (US)
560. *Syringodium filiforme*, 15 (US)
561. "*Epidendrum bifidum*," 5
562. *Ponthieva glandulosa*, 6 (US)
563. *Epidendrum wrightii*, 21 (US)
564. "*Epidendrum broughtonioides*," 6
565. "*Polystachya luteola*"
566. *Oncidium variegatum*, 19 (US)
566A. "*Epidendrum bifidum*"
567. "*Cranichis muscosa*"
568. "*Spiranthes apiculata*," 6
569. *Ponthieva ekmanii*, 5 (US)
570. "*Epidendrum nocturnum*," 22
571. *Epidendrum strobuliferum*, 19 (US)
572. "*Aeranthus* sp.," 19
573. *Epidendrum difforme*, 19 (US)
574. *Bletia patula*, 5 (GH, US)
574A. *Bletia patula* (US)
575. *Xyris caroliniana*, 6 (US)
576. *Cyperus peruviana*, 9 (US)
577. *Cyperus densicaespitosus*, 19 (US)
578. "*Rhynchospora florida*," 21
579. *Cyperus haspan*, 6 (US)
580. "*Scirpus exiguus*," 6
581. *Rhynchospora barbata* (US)
582. *"*Eleocharis* sp. nov."[35]
583. *Rhynchospora barbata* (US)
584. "*Fimbristylis brizoides*," 6
585. "*Rhynchospora barbata*"
586. blank
587. *Eleocharis capitata*, 9 (US)
588. "*Rhynchospora vahliana*"
589. "*Rhynchospora glauca*," 19
590. *Fimbristylis dichotoma*, 6 (US)
591. *Rhynchospora barbata* (US)
592. *Eleocharis retroflexa*, 19 (US)
593. *Cyperus nanus*, 15 (US)
594. *Scleria secans*, 19 (US)
595. *Cyperus elegans*, 15 (US)
596. *Eleocharis geniculata* (US)
597. "*Eleocharis plantagineus*," 19
598. *Fuirena umbellata*, 19 (US)
599. *Rhynchospora pusilla*, 19 (US)
600. *Eleocharis chaetaria*, 6 (US)
601. "*Dichromena pusilla*," 19
602. "*Kyllingia brevifolia*," 19
603. *Mayaca fluviatilis*, 6 (US)
604. "*Carex scabrella*," 15
605. *Pharus latifolia* (US)
606. "*Pharus latifolius*," 19
607. *Paspalum laxum*, 19 (US)
608. *Ichnanthus pallens*, 19 (US)
609. "*Paspalum compressum*," 19
610. *Chloris sagraeana*, 19 (US)
611. *Eragrostis ciliaris*, 19 (US)
612. *Chloris inflata* (US)
613. "*Orthopogon labiaceus*," 19
614. *Lasiacis patentiflora*, 19 (US)
615. *Lasiacis sloanei*, 19 (US)
616. **Hyparrhenia hirta*, 12 (US)
617. *Paspalum laxum* (US)
618. *Paspalum laxum* (US)
619. *Phragmites communis* (US)
620. *Paspalum virgatum*, 19 (US)
621. *Cenchrus brownii* (US)
622. *Digitaria villosa* (US)
623. *Reynaudia filiformis*, 6 (US)
624. "*Cenchrus viridis*," 19
624A. *Panicum stenodes*, 6 (US)
625. *Andropogon virgatus*, 6 (US)
626. *Arundinella confinus*, 6 (US)
627. *Panicum diffusum*, 21 (US)
628. "*Tricholaena insularis*"

[34] The available material of these palms is inadequate for accurate determination.

[35] A specimen collected in "springy places in savannas of the interior, Feb. 10," according to Wright's manuscript. No specimens have been located.

629. *Andropogon bicornis* (US)
630. *Tricholaena insularis* (US)
630. *Paspalum paniculatum* (US)
631. **Andropogon saccharoides*, 6 (US)
632. **Andropogon saccharoides*, 6 (GH, US)
633. *"Panicum dichotomum,"* 21
634. *Digitaria horizontalis*, 19 (US)

Series II

1. *"Lycopodium mexicanum"*
2. *Ananthacorus angustifolia* (US)
3. *Adiantum deltoideum* (US, YU)
4. *Adiantum cristatum* (US, YU)
5. *Adiantum obliquum* (US, YU)
6. *Lindsaea portoricensis* (US)
7. *Adiantum fragile* (US, YU)
8. *Dryopteris serra* (US, YU)
9. *Pteris longifolia* (US, YU)
10. *Pityrogramma tartarea* (US, YU)
11. *"Gleichenia pubescens"*
12. *Dryopteris tetragona* (YU)
13. *Polypodium salicifolium* (US)
14. *Polypodium astrolepis* (US)
15. *Aspidium scolopendrioides* (YU)
16. *Tectaria heracleifolia* (US)
17. *Tectaria martinicensis* (US, YU)
18. *Pityrogramma sulphurea* (US, YU)
19. *Trichomanes krausii* (US, YU)
20. *Trichomanes lineolatum* (US)
21. *Trichomanes krausii* (US)
22. *Anemia hirsuta* (YU)
23. *Anemia adiantifolia* (YU)
24. *Cheilanthes microphylla* (US, YU)
25. *Asplenium serratum* (US, YU)
26. *Alsophila aquilina* (US)
27. *Cyclopeltis semicordata* (US, YU)
28. *Asplenium dentatum* (US)
29. *Pityrogramma calomelaena* (US, YU)
30. *Asplenium cristatum* (US)
31. *Dryopteris dentata* (US)
32. *Cyathea arborea* (US, YU)
33. *Odontosoria aculeata* (US, YU)
34. *Alsophila aquilina* (US)
35. *Selaginella plumosa* (US, YU)
36. *Lycopodium cernuum* (US, YU)
37. *"Lycopodium complanatum"*

Series III

Aristolochia aff. *pentandra* [36] (K)
Bidens leucantha (US)
Guazuma ulmifolia (US)
Hura crepitans, 19 (US)
Hymenaea courbaril (US)
Ipomoea batatas, 19 (US)
Ipomoea pes-caprae (US)
Iresine celosia (US)
Juniperus gracilis (US)
Mimosa pudica (US)
Nopalea cochenillifera, 10 (GH)
Pinus occidentalis (US)
Vaccinium meridionale [37] (US)
Zamia pumila (US)

Series IV

Ananas sativus, 19
Annona cherimola
Annona muricata
Annona palustris
Sebastiana corniculata, 9

[36] Determination by Oliver, 1871.
[37] Probably collected near Cinchona, Jamaica.

COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, II

STRUCTURE AND DISTRIBUTION OF SCLERENCHYMA IN THE PHLOEM OF PERESKIA, PERESKIOPSIS AND QUIABENTIA

I. W. BAILEY [1]

VARIOUS FORMS OF SCLERENCHYMA, as commonly defined (e.g., Eames and MacDaniels,[2] Esau [3]), occur in the leaf-bearing genera *Pereskia*, *Pereskiopsis* and *Quiabentia*: (1) libriform fibers are present in the secondary xylem of stems and roots, (2) strands of aggregated slender fibers in the primary phloem of stems, (3) concentric layers of sclereids in periderm of stems and roots, and (4) highly diversified forms of sclereids in the secondary phloem of *Pereskia*. It is significant in this connection that, under normal circumstances, sclerenchyma does not occur in the leaves and pith of the three genera. The libriform fibers of the xylem and the sclereids of the periderm will be dealt with in subsequent papers of this series. In the following pages, I shall confine myself to a discussion of sclerenchymatous elements that are formed in the phloem of the three genera.

The leaf-bearing Cactaceae have mixtures of very dense and exceedingly soft tissues and are difficult to section. After experimenting with various methods of embedding following preliminary softening with such reagents as hydrofluoric acid, I have in general obtained the most useful preparations by sectioning stems and roots of living plants or specimens preserved in formalin-acetic-alcohol fixative without the use of preliminary treatments. Although the transverse and longitudinal sections thus obtained with an adequately sharpened knife and sliding microtome are relatively thick, they are suitable for critical visual examination. Furthermore, they have the advantage, not only of being obtained simply and rapidly, but also of retaining starch, crystals, and other cell inclusions which may be much modified or eliminated during softening and embedding. It must be admitted, however, that they are not of the best quality for photographic illustration.

FIBERS OF THE PRIMARY PHLOEM

Strands of aggregated primary phloem fibers occur in the stems of *Pereskiopsis* and *Quiabentia*, as well as in those of *Pereskia* (FIGS. 1a,

[1] This investigation was financed by a grant from the National Science Foundation.

[2] Eames, A. J., and L. H. MacDaniels. An introduction to plant anatomy. Ed. 2. McGraw-Hill Book Co., N. Y., 1947.

[3] Esau, K. Plant Anatomy. John Wiley and Sons, N. Y., 1953.

7a). Particularly in the more succulent parts of *Quiabentia* and some species of *Pereskiopsis*, the number of fibers in each strand tends to be reduced. Furthermore, the maturation of fibers in the former genera tends to be precocious, whereas in *Pereskia* the final stages of maturation may at times be delayed until more or less extensive cambial activity has occurred.

The individual fibers are slender, elongated elements of the general external form illustrated in FIG. 12. Their diameter commonly varies from 20 to 50 microns and their length from a few hundred microns to more than 2000. The marked variability in length occurs, not only in strands from different parts of a plant, but also in adjacent fibers of a single strand. Fibers having normal, lignified secondary walls may be internally septate or nonseptate, but they do not store starch as the corresponding septate and nonseptate libriform fibers of the secondary xylem so commonly do. Those of *Quiabentia* and *Pereskiopsis* tend to form relatively thick secondary walls and contain few if any internal septa at maturity (FIG. 13). On the contrary, in the case of *Pereskia*, many of the fibers have thinner secondary walls and are internally septate (FIG. 14). It is significant that part or all of such septate fibers in a strand may ultimately form internally a chain of sclereids having lignified, multilayered walls (FIG. 15). Occasionally, the protoplast of one of the sclereids may divide leading to the formation of two smaller sclereids included within a larger one. This unusual phenomenon of cells-within-cells, which is of infrequent and sporadic occurrence in septate libriform fibers of secondary xylem (FIG. 6) is of considerable interest from physiological and developmental points of view and merits detailed investigation. For example, the two or three successive waves of lignified wall formation indicate that lignification is not necessarily an immediate precursor of loss of potentialities or degeneration of the protoplast as has sometimes been assumed.

The orientation of cellulosic microfibrils in the broad central or S_2 layer of the secondary wall of septate and nonseptate fibers, of both the primary phloem and the secondary xylem, varies from approximate parallelism to the long axis of the cell to helices of varying pitch. Clues to such variations may be obtained by studying the orientation of the slit-like pits, by the distribution of slip-planes, and by examining thin transverse, longitudinal and diagonal sections in polarized light. In FIG. 6, a very thin, perfectly transverse section in polarized light between crossed nicols, the tenuous outer or S_1 layer of the four adjacent fibers is strongly birefringent. The broad central or S_2 is dark, whereas in longitudinal section it is birefringent. This indicates that the orientation of cellulosic microfibrils in the S_2 layer of the secondary wall is approximately longitudinal, as does the orientation of slit-like pits and the distribution of slip-planes visible in longitudinal sections. Internal to the normal S_1 and S_2 layers of the septate fibers in FIG. 6 are transverse sections of the multilayered walls of included sclereids, the cellulosic layers of which are alternatingly birefringent and dark in polarized light. In such transverse sections as

FIG. 6, it is not possible to determine whether the original secondary wall of the fibers has a tenuous S_3 layer or not. It should be emphasized in this connection that these cells-within-cells provide interesting material for analysis by electron microscopy.

Occasionally a cell of prosenchymatous form on the margins of a strand of primary phloem fibers divides precociously before secondary wall formation (FIG. 16). Subsequently such cells may form a chain of sclereids (FIG. 17) comparable developmentally to wood parenchyma strands or the strands of short tracheids that occur in certain of the Pinaceae. (See glossary of terms used in describing woods.[4])

FORMS OF SCLERENCHYMA IN THE SECONDARY PHLOEM OF PERESKIA

Under normal conditions of growth, schlerenchyma does not occur in the cortex and secondary phloem of stems and roots of species of *Pereskiopsis* and *Quiabentia* that I have investigated. In striking contrast to absence in these genera is the occurrence (particularly in larger stems and roots) of more or less numerous and diversified forms of sclereids in the secondary phloem of all species of *Pereskia* (including *Rhodocactus*) of which I have examined adequate material. The form and the distribution of the sclereids is consistently different in three distinct categories of putative species of *Pereskia*.

1. Species with Diffusely Distributed Sclereids in the Secondary Phloem

In *Pereskia aculeata* Mill., *P. pititache* Karw., *P. conzattii* Britt. & Rose, *P. autumnalis* (Eichlam) Rose, *P. nicoyana* Web., *P. weberiana* K. Schum., and *P. diaz-romeroana* Cárd., the sclereids in the secondary phloem of large stems and roots are abundant and diffusely distributed (FIGS. 1–3). In transverse sections, these cells, which vary in diameter from less than 18 to more than 100 microns, have conspicuously multilayered secondary walls which frequently occlude the lumen of the cell. As indicated in FIG. 5, the numerous layers of the secondary wall (which may exceed 50 in the case of the largest cells) are alternatingly birefringent and dark or feebly birefringent in polarized light. (Compare with the internal sclereids shown in FIG. 6.)

As seen in longitudinal sections (FIG. 4), these cells have a much elongated prosenchymatous form, the most slender ones having a length of a few hundred microns, whereas the broadest ones may attain at times a length of more than two thousand microns. In many of these cells the lumen tends to be occluded toward the ends of the cells and to be much reduced in the central part (FIG. 18). However, some of the cells having thinner multilayered walls become septate and may subsequently form a

[4] International Association of Wood Anatomists. Glossary of terms used in describing woods. Tropical Woods **36**: 1933.

chain of shorter sclereids internally. The pits of the secondary wall tend to be restricted to the broadest central part of the cell (Fig. 18) and to be more or less irregularly distributed. It is significant in this connection that many of the pits are of the so-called ramiform type characteristic of many sclereids (Fig. 19). From a developmental point of view, such pits are actually of a coalescing, rather than of a ramifying type, for, the orifices of two or more simple pits in the first-formed layers of the secondary wall unite to form a single opening in the inner or last-formed layers of the wall.

A limited number of sclereids may occur at times in the expanded cortex of much enlarged stems (Fig. 1b). These vary from cubical to various bizarre forms. However, where they have a conspicuously longer axis, it is oriented at various angles and not consistently parallel to the long axis of the stem.

2. Species with Sclereids Aggregated in Longitudinally Oriented Clusters

In large older stems of *Pereskia sacharosa* Griseb., *P. grandifolia* Haw., *P. bleo* DC., *P. corrugata* Cutak, and *P. tampicana* Web. aggregations of sclereids commonly occur in the secondary phloem (Figs. 7, 8). These aggregations, as seen in longitudinal sections of the stem, are of elongated form, frequently of more or less fusiform outline (Fig. 9), and are oriented parallel to the long axis of the stem. They are composed of sclereids which vary markedly in size, form and complexity of internal structure. Although in general the sclereids have a more or less extensively elongated form (with their major axis oriented parallel to the long axis of the stem), they frequently assume aberrant shapes (Fig. 23), apparently due to pressures exerted by adjacent cells during the earlier stages of their excessive enlargement. In some cases, the sclereids have a thick, lignified, multilayered wall and a much restricted or occluded lumen (Fig. 20). In other cases, the sclereids first form a multilayered wall followed by transverse septation and subsequent differentiation of two, three, or more smaller sclereids internally (Fig. 21). Particularly in the case of the largest sclereids, which may attain a diameter of 200 microns and a length of 1000 microns, the protoplasts of the included sclereids may in turn divide, leading to the formation of a second set of still smaller sclereids (Fig. 22). Such compound sclereids of the cells-within-cell type commonly assume many diverse forms internally depending upon the timing and frequency of internal divisions and upon the frequency of diagonally rather than transversely oriented septa. Therefore, in macerations of the phloem, it may be difficult at times to determine with certainty whether certain of the smaller isolated sclereids developed directly from less expanded parenchymatous elements of the secondary phloem or have been released from large compound sclereids by the disrupting forces of maceration.

Strands of aggregated sclereids, at least in many cases, are infrequent

or absent, even in much enlarged roots of this category of pereskias, and commonly do not occur in young stems. Thus, I suspect that such pereskias as *Pereskia bahiensis* Gürke and *P. moorei* Britt. & Rose, which have very large, relatively thin, characteristically pinnately veined leaves, will ultimately prove to belong in this category of species when adequate material of the largest and oldest stems can be obtained and studied.

3. Species with Ordinary "Stone Cells" Aggregated in Massive Irregular Clusters

In both the secondary phloem and cortex of older stems and roots of *Pereskia colombiana* Britt. & Rose, *P. guamacho* Web., *P. cubensis* Britt. & Rose, and *P. portulacifolia* Haw., simple, comparatively small sclereids occur in more or less massive aggregations of irregular form (PLATE IV). As indicated in longitudinal sections (FIG. 11), these aggregations do not have a consistently elongated form oriented parallel to the long axis of the stem or root. Furthermore, the sclerotic masses do not contain large compound sclereids but are composed of ordinary "stone cells" as regards size and form. These typical "stone cells" have profusely pitted, thick, lignified, multilayered walls (FIGS. 24–26). When they have a conspicuous major axis (FIG. 26), it tends to be oriented at right angles to, rather than parallel with, the long axis of the stem or root. It is evident from a developmental point of view that these sclereids differentiate from parenchymatous elements of the cortex and secondary phloem without excessive expansion and without internal septation.

DISCUSSION AND CONCLUSIONS

The occurrence of various forms of sclereids in the secondary phloem of pereskias and the absence of such cells in comparable tissue of *Pereskiopsis* and *Quiabentia* are obviously of some significance from a generic point of view, and parallel the presence or absence of glochids in these leaf-bearing genera. However, such differences must ultimately be considered in relation to close similarities that occur in other cells, tissues, and parts of the plants. Obviously a synthesizing discussion should be deferred to the last paper of this review.

The consistent differences in the form and distribution of sclereids in three distinct categories of pereskias are of considerable taxonomic significance, not only in the discussion of putative genera, e.g., *Rhodocactus*, but also in dealing with putative species and varieties. Evidence from the first category of pereskias is indicative of relationship of *Pereskia aculeata* to *P. diaz-romeroama* and *P. weberiana*, of Bolivia, and likewise to *P. conzattii*, of Southern Mexico, and *P. autumnalis* and *P. nicoyana*, of Central America. Evidence from the second category of pereskias is indicative of affinities between *P. sacharosa*, *P. grandifolia*, *P. bleo*, *P. corrugata*, and *P. tampicana*; that from the third category of pereskias of affinities between *P. colombiana* and *P. guamacho*, of northern South

America, and the West Indian endemics *P. cubensis* and *P. portulacifolia*.

The elongated or prosenchymatous form of the sclerenchymatous elements in the first category of pereskias raises the question whether the cells should be classified as phloem fibers with lignified, multilayered secondary walls or as elongated forms of sclereids. The occurrence of "ramifying" or coalescing simple pits in the thick secondary walls of these cells is a characteristic feature of many sclereids rather than of typical fibers. Furthermore, there are numerous transitions between short and variously elongated sclereids in the second category of pereskias. Admittedly, it is difficult to classify plant cells in rigid compartments, owing to the frequent occurrence of intergrading or transitional forms of morphological characteristics. However, in view of the well-known diversities in the size and form of sclereids (see Foster [5]) I am inclined to refer to more or less elongated cells in *Pereskia* having thick, lignified, multilayered walls with "ramiform" or coalescing pits as elongated forms of sclereids rather than as fibers.

The frequent occurrence of sclereids within fibers of the primary phloem and the formation of successive generations of smaller sclereids within large ones of the secondary phloem provide significant material for physiological and developmental investigations, as well as electron microscopy.

ACKNOWLEDGMENTS

I am indebted to the American Philosophical Society for the loan of a Wild microscope. Since acknowledging the assistance of various individuals in the first paper of this series, I have received material of *Pereskia sacharosa* from Dr. Abraham Willink and of *P. portulacifolia* from Dr. José Jiménez. I am greatly indebted to these individuals for the time and effort involved in securing adequately preserved specimens for me. The drawings in this and the preceding paper of this series were made by Mr. Elmer W. Smith.

EXPLANATION OF PLATES

PLATE I

FIGS. 1–3. DIFFUSE DISTRIBUTION OF SCLEREIDS IN TRANSVERSE SECTIONS OF STEMS. 1, *Pereskia aculeata* [AW 9912] cluster of primary phloem fibers at A, a sclereid in the cortex at B, × 80. 2, *P. nicoyana* [*Rodriguez 662*], × 80. 3. *P. diaz-romeroana* [*Cárdenas*], × 80.

[5] Foster, A. S. Practical plant anatomy. Ed. 2. D. Van Nostrand Co., N. Y., 1949.

PLATE II

FIGS. 4–6. FREE AND INCLUDED SCLEREIDS. 4, *Pereskia nicoyana* [*Rodriguez 662*], longitudinal section of a stem showing elongated diffusely distributed sclereids in the secondary phloem, × 80. 5, *P. aculeata* [Aw 9912], transverse section of a sclereid in polarized light between crossed nicols, × 260. 6, Transverse section of septate fibers with included sclereids photographed in polarized light between crossed nicols, × 1200.

PLATE III

FIGS. 7–9. AGGREGATED SCLEREIDS OF THE SECOND CATEGORY OF PERESKIAS. 7, *Pereskia grandifolia* [*Castellanos*], transverse section showing two aggregations of sclereids in the secondary phloem, primary phloem fibers at A, × 80. 8, *P. sacharosa* [Tucumán], transverse section of a stem showing aggregation of sclereids in the secondary phloem, × 80. 9, *P. grandifolia* [*Castellanos*], longitudinal section of the secondary phloem showing elongated aggregation of sclereids, × 80.

PLATE IV

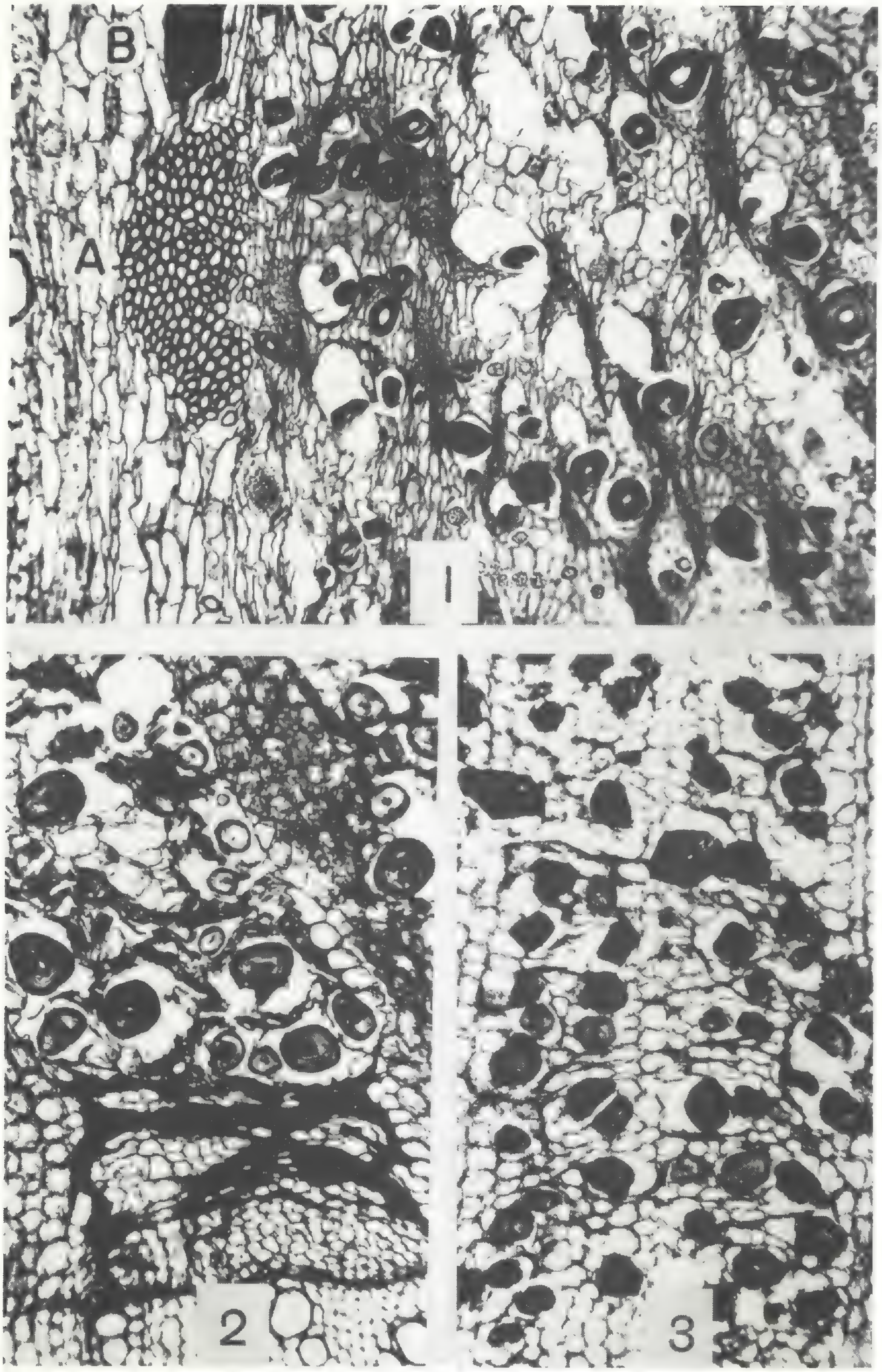
FIGS. 10–11. AGGREGATIONS OF "STONE CELLS" IN THE THIRD CATEGORY OF PERESKIAS. 10, *Pereskia cubensis* [Atkins Garden], transverse section of a root showing massive clusters of sclereids in the secondary phloem, × 80. 11, *P. guamacho* [*Steyermark*], longitudinal section of a stem showing irregular masses of sclereids in the outer secondary phloem and cortex, × 80.

PLATE V

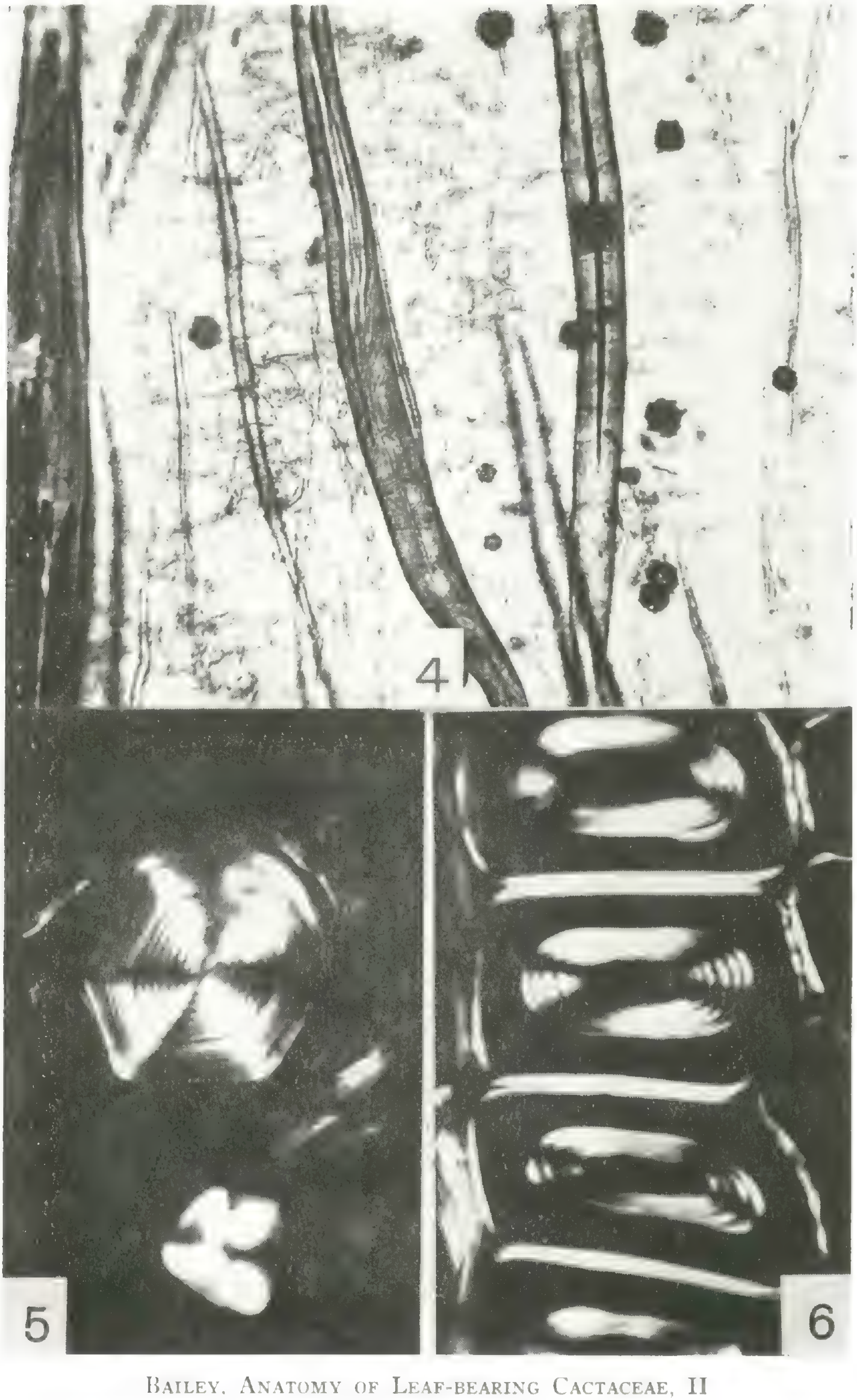
FIGS. 12–17. DIAGRAMMATIC ILLUSTRATIONS OF PRIMARY PHLOEM FIBERS AND SCLEREIDS. Included protoplasts are stippled, primary walls and septa are black, first-formed secondary walls of fibers are white, and the secondary walls of sclereids are multilayered. 12, Characteristic form of immature primary phloem fibers prior to secondary wall formation. 13, Part of a nonseptate fiber having thick secondary wall and reduced lumen. 14, Part of a septate fiber having a relatively thin secondary wall. 15, Part of a septate fiber with included sclereids. 16, Precocious septation of an elongated cell prior to the formation of strand sclereids shown in Fig. 17.

PLATE VI

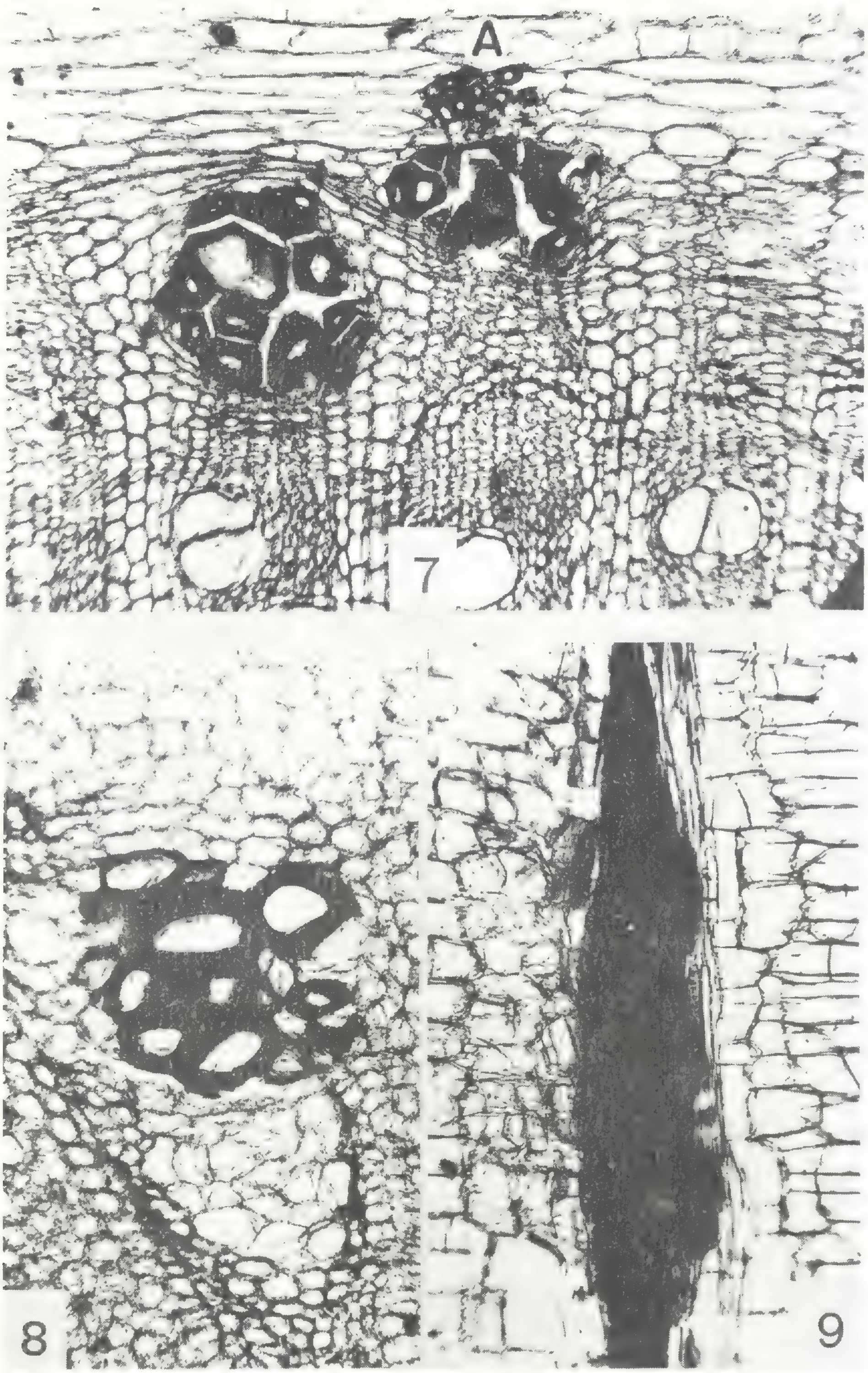
FIGS. 18–26. DIAGRAMMATIC ILLUSTRATION OF THE FORMS OF SCLEREIDS IN THREE CATEGORIES OF PERESKIAS. Included protoplasts are stippled, primary walls and septa are black, and the secondary walls of sclereids are multilayered. 18, Form of elongated, nonseptate sclereids in the first category of pereskias. 19, Part of the secondary wall of such a sclereid showing "ramiform" or coalescing pits. 20, Single, nonseptate sclereid from an aggregation in the second category of pereskias. 21, Compound sclereid from the same source showing three septa and four included smaller sclereids. 22, Doubly compound sclereid from the same source showing septation of such included sclereids as illustrated in Fig. 21 and the maturation of a second set of still smaller included sclereids. 23, Small laterally deformed sclereid. 24–26, Typical "stone cells" from aggregations in the third category of pereskias.



BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, II



Bailey, Anatomy of Leaf-bearing Cactaceae, II



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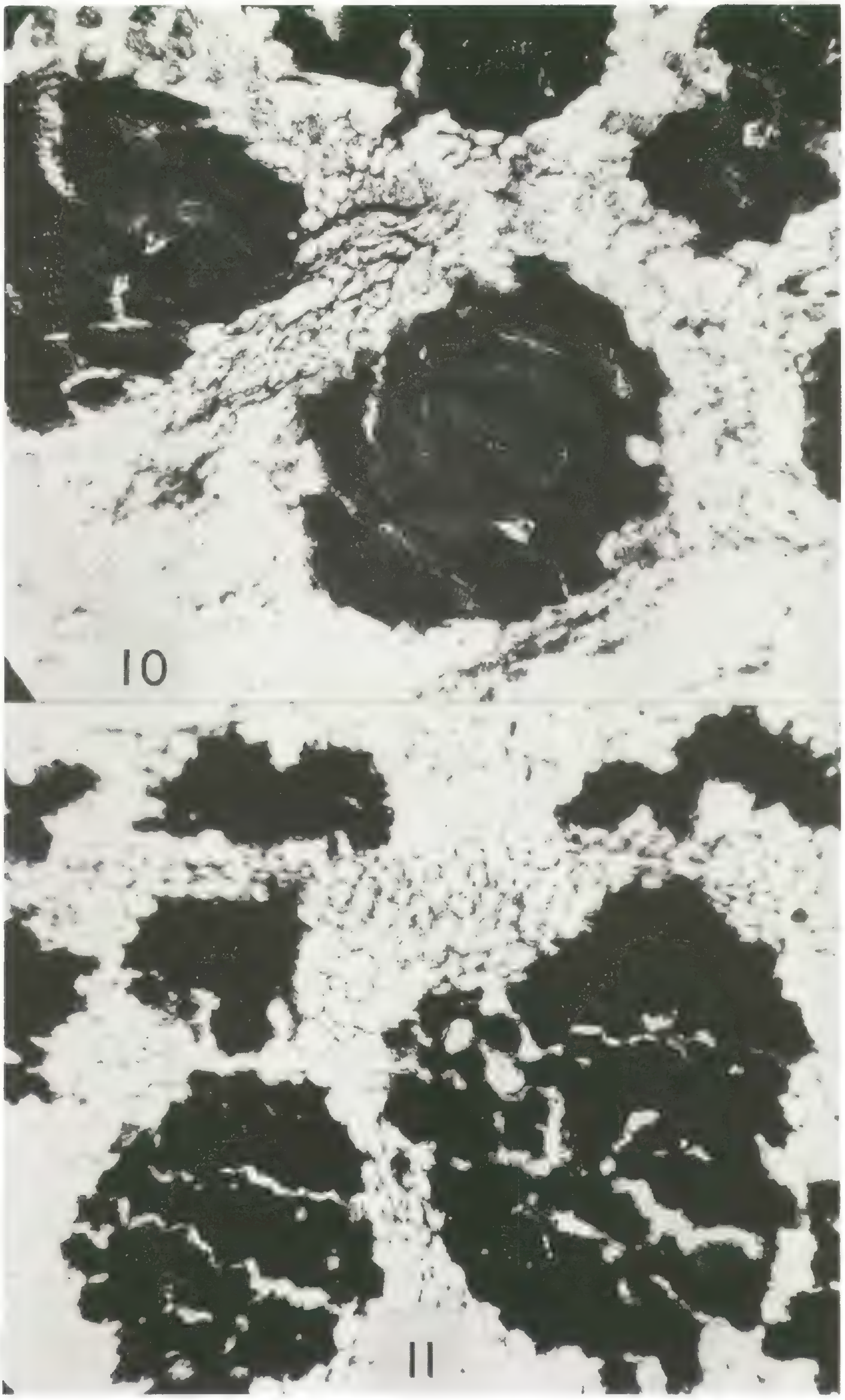
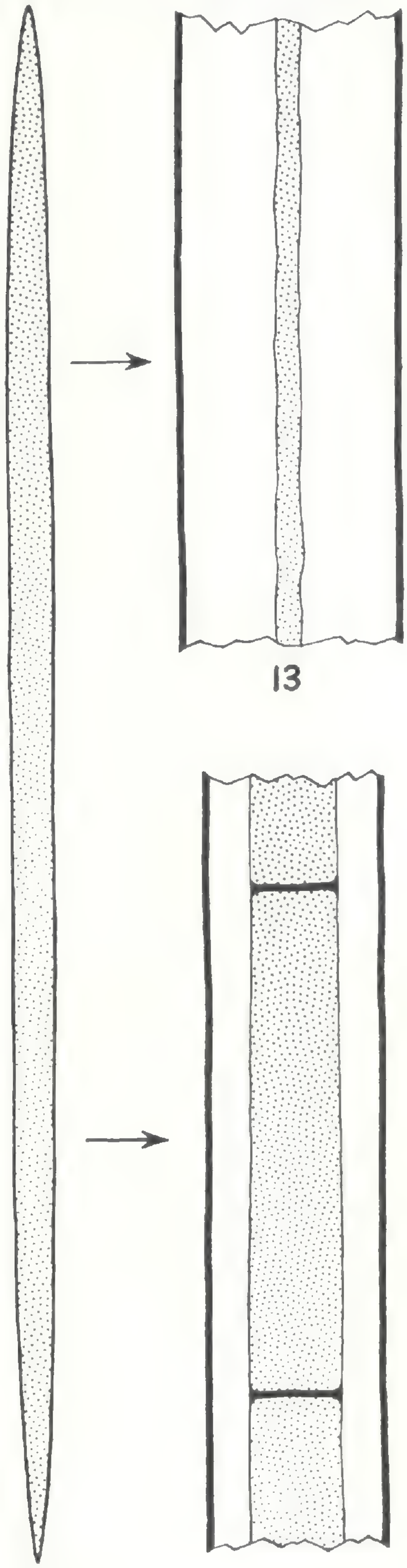


BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, II



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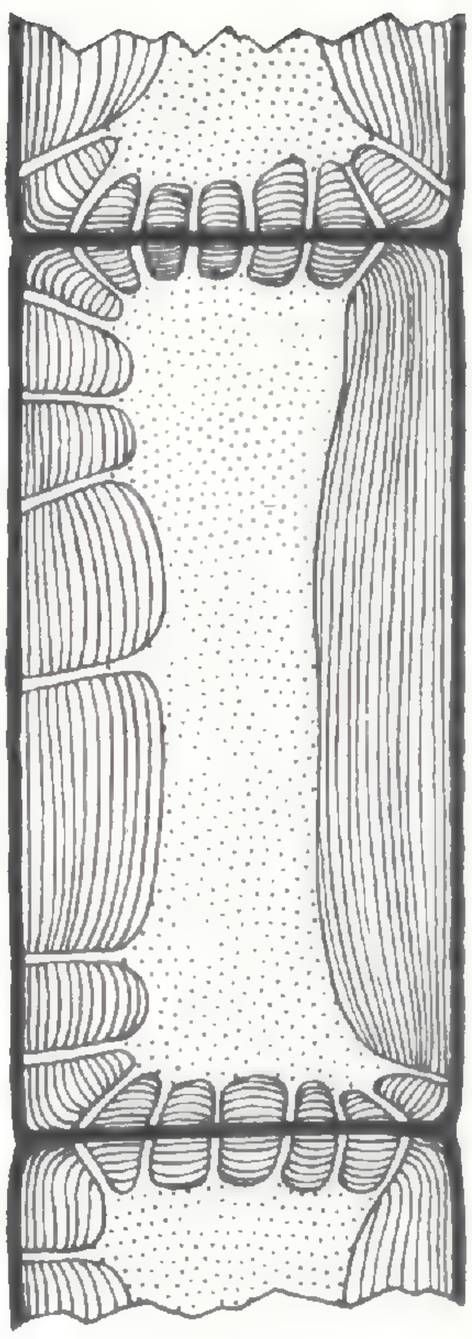

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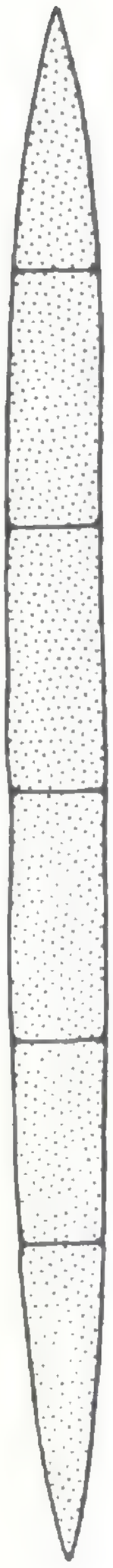

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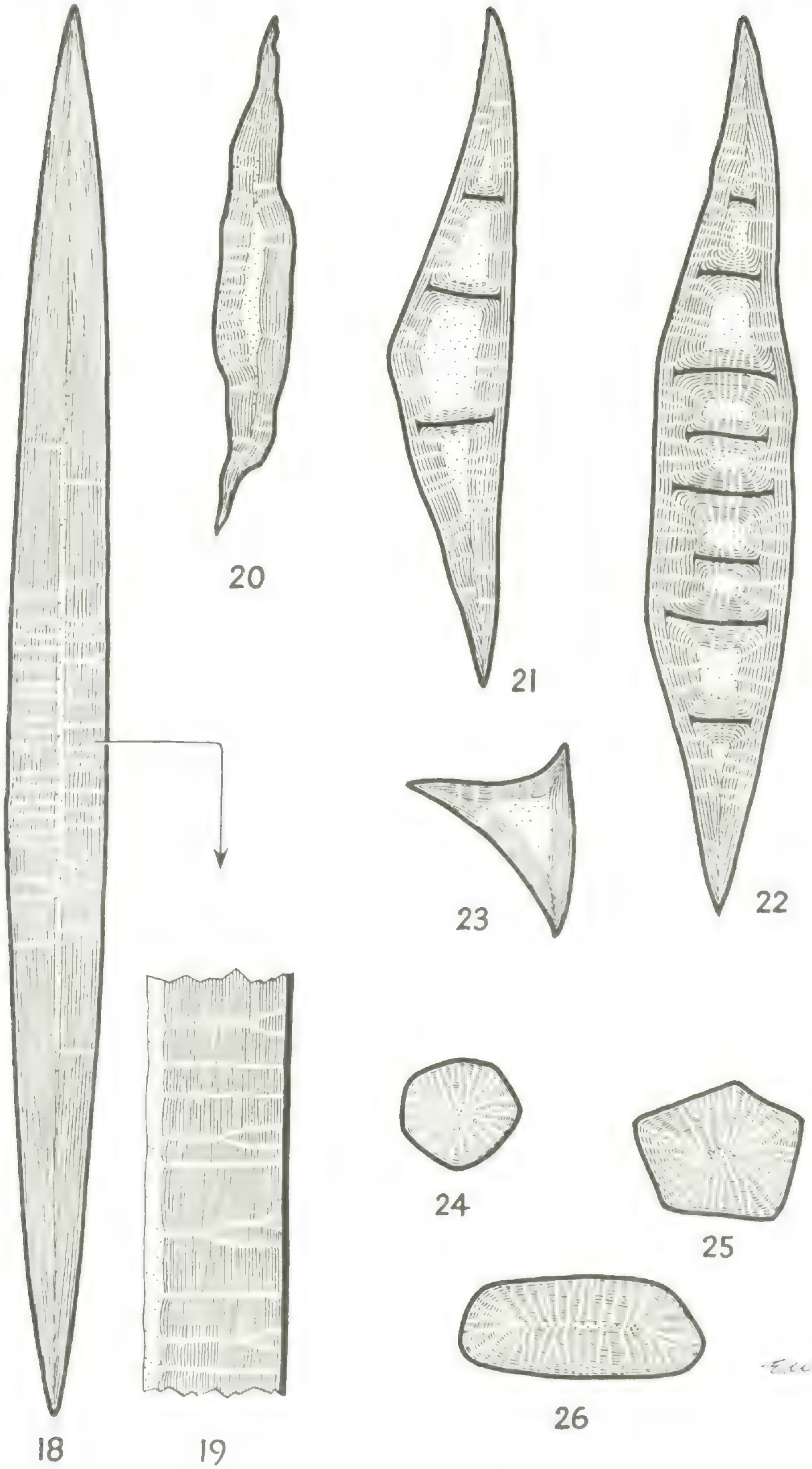
BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, II



BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, II

THE CYTOLOGY OF SOME CULTIVATED SPECIES OF VIBURNUM

JOAB L. THOMAS

VIBURNUM has long been recognized as a difficult group taxonomically, and more recently it has been shown to be somewhat complex cytologically. In recent years evidence from cytological studies has been used extensively in formulating taxonomic conclusions, but all too often only a small percentage of the species in a genus is studied cytologically, and, on the basis of these, generalizations are made concerning the entire genus. This has led to erroneous conclusions, both in cytology and taxonomy. It is hoped that additional studies in *Viburnum* will lead to a better understanding of the cytology of the genus, and that this, in turn, can be used in developing a sound and workable taxonomy.

The first chromosome counts in *Viburnum* were published in 1930 by Sax and Kribs (5) in a study of the cytology and wood structure in the Caprifoliaceae. In this paper chromosome numbers were reported for eleven species of *Viburnum* representing six of the nine sections of the genus, according to the classification of Rehder (3), and including both Asiatic and American species. All of the species included in this study were found to have nine pairs of chromosomes. However, in 1932, Simonet and Miedzyrzecki (6) reported that *Viburnum fragrans* has only eight pairs of chromosomes and, in 1936, Sugiura (7) reported that *V. awabuki* (*V. odoratissima*) has ten pairs of chromosomes. The most comprehensive study of the chromosomes of *Viburnum* was that of Janaki Ammal (1) in which a survey was made of the species growing in the botanical gardens at Wisley, Kew, and Paris. In this paper, chromosome counts were reported for the first time for twenty-three species and varieties, and additional counts were given for sixteen species for which counts had been reported previously by other authors. The present study was undertaken to extend the survey of chromosome numbers in *Viburnum* and to see if further evidence could be obtained on the origin of the aneuploid series in the genus. The chromosome counts obtained in this study, along with all other counts for *Viburnum* which I have seen, are listed in TABLE I. The classification used in this table is based on that of Rehder (4).

MATERIALS AND METHODS

The plant materials used in this study were from the living collection on the grounds of the Arnold Arboretum. Most of the chromosome counts were made from acetocarmine squashes of pollen mother cells. Satisfactory preparations were obtained by squashing fresh, whole anothers on a dry

TABLE I. **Chromosome Counts in Viburnum.**

SPECIES	*2n*	AUTHORITY *	DOCUMENTATION †	DISTRIBUTION
Sect. THYRSOSMA				
V. erubescens Wall.	48	1	none	Himal., w. China
V. foetens Decne.	16	1	none	Himal., Kashmir
V. fragrans Bunge	16	1, 6	none	n. China
var. *candidissima*	16	8	55–50–B	cult.
var. *alba*	32	1	none	n. China
V. grandiflorum Wall.	16	1	none	Himal.
V. henryi Hemsl.	48	1	none	centr. China
V. odoratissimum Ker-Gawl.	40	1	none	India, China
V. seiboldii Miq.	16	1	none	Japan
"	32	8	AA616–6–B	"
V. suspensum Lindl.	16	1	none	Liukiu Islands
Sect. LANTANA				
V. bitchiuense Makino	16	1	none	w. Japan
V. buddleifolium Wright	20	1	none	centr. China
"	18	6	none	"
V. × *burkwoodii* Burkwood & Skipwith (*V. carlesii* × *utile*)	18	8	AA815–41–B	cult.
V. × *carlcephalum* Burkwood ex. Pike (*V. carlesii* × *macrocephalum*)	18	8	AA618–53–A	cult.
V. carlesii Hemsl.	20	1	none	Korea
"	18	2, 6, 8	AA17981–A	"
V. cotinifolium D. Don	18	2	none	Himal.
V. lantana L.	18	1, 2, 5	none	Eur., w. Asia
var. *rugosum* Lange	18	8	AA907–27–A	cult.
V. mongolicum (Pall.) Rehd.	16	1	none	e. Siberia, n. China
V. × *rhytidophylloides* Suringar (*V. rhytidophyllum* × *lantana*)	18	8	AA711–36–B	cult.
V. rhytidophyllum Hemsl.	18	1, 6	none	centr. & w. China
V. utile Hemsl.	18	1	none	centr. China
V. urceolatum Seib. & Zucc.	18	8	AA876–51	Japan
V. veitchii Wright	18	8	AA7198	centr. China
Sect. PSEUDOTINUS				
V. alnifolium Marsh.	18	1, 5	none	e. N. Am.
V. furcatum Blume ex Maxim.	18	1	none	Japan
Sect. PSEUDOPULUS				
V. plicatum Thunb.	16	8	AA18016–1	Japan, China
f. *lanceatum* Rehd.	16	8	AA6122–1	cult.
f. *mariesii* (Veitch) Rehd.	18	8	AA870–51–A	cult.
f. *roseum* (Doney) Rehd.	16	8	AA856–34	cult.

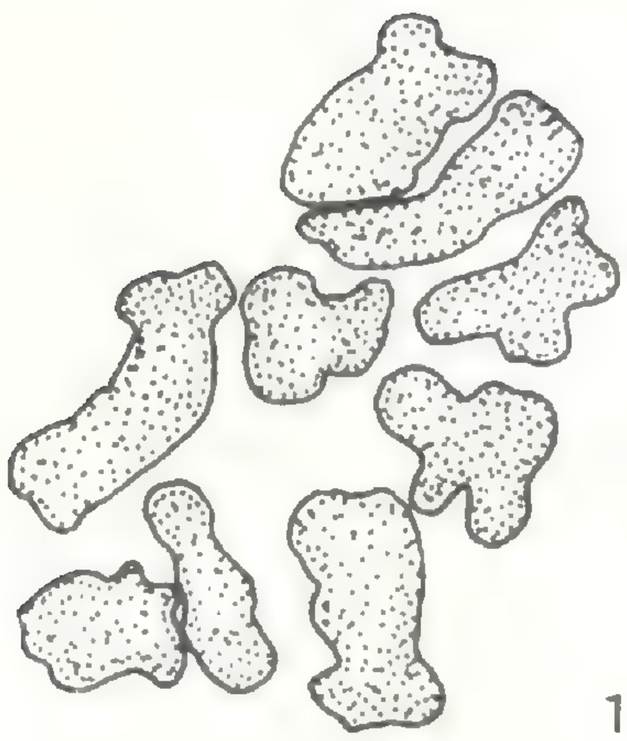
TABLE I (*Continued*)

SPECIES	2*n*	AUTHORITY *	DOCUMENTATION †	DISTRIBUTION
Sect. LENTAGO				
V. cassinoides L.	18	8	AA17997	e. N. Am.
V. lentago L.	18	1, 5	none	e. N. Am.
V. nudum L.	18	1	none	e. N. Am.
V. prunifolium L.	18	1, 5	none	e. N. Am.
Sect. TINUS				
V. cinnamomifolium Rehd.	18	1	none	w. China
V. davidii Franch.	18	1	none	w. China
V. harryanum Rehd.	18	2	none	w. China
V. propinquum Hemsl.	18	2	none	centr. & w. China
V. tinus L.	36	1, 2, 6	none	se. Eur.
Sect. ODONTOTINUS				
V. acerifolium L.	18	1, 5	none	e. N. Am.
V. betulifolium Batalin	18	1	none	centr. & w. China
V. dentatum L.	54	1	none	e. N. Am.
"	36	8	AA17985	"
var. *pubescens* Ait.	36	8	AA18009	"
V. dilatatum Thunb.	18	8	AA229–46–B	e. Asia
f. *hispidum*	18	8	AA17486–1–A	cult.
f. *xanthocarpum* Rehd.	18	8	AA10140	cult.
V. foetidum Wall.	16	1	none	w. China
var. *rectangulatum* (Graebn.) Rehd.	16	1	none	w. China
V. hirtulum Rehd.	18	8	AA708–37–B	China
V. hupehense Rehd.	18	5, 6	none	China
V. lobophyllum Graebn.	20, 22	1	none	centr. & w. China
"	18	5	none	"
V. molle Michx.				
f. *leiophyllum* Rehd.	18	8	AA4643–1–A	e. N. Am.
V. ovatifolium Rehd.	18	1, 8	AA20078A	w. China
V. pubescens Pursh	36	8	AA18008	e. N. Am.
V. raffinesquianum Roem. & Schult. var. *affine* (Schneid.) House	20	8	AA4622–2–B	e. N. Am.
V. setigerum Hance	36	8	AA20189	centr. & w. China
" (as *V. theiferum* Rehd.)	18	6	none	"
f. *aurantiacum* Rehd.	36	8	AA812–32	"
V. wrightii Miq.	16	1	none	Japan
Sect. OPULUS				
V. opulus L.	18	1, 5	none	Eur. & n. Africa
f. *xanthocarpum* (Endl.) Rehd.	18	8	AA1298–28–A	cult.
V. sargentii Koehne	18	5	none	ne. Asia
f. *calvescens* (Rehd.) Rehd.	18	8	AA467–26	cult.
V. trilobum Marsh.	18	1, 5	none	n. N. America
'compactum'	18	8	AA871–51	cult.

* 1, Janaki Ammal; 2, Poucques; 5, Sax; 6, Simonet and Miedzyrzecki; 7, Sugiura; 8, Thomas, reported here for the first time.

† The numbers listed under this column are the accession numbers for the plants in the living collection of the Arnold Arboretum. Voucher specimens of these plants bearing the accession number have been deposited in the herbarium of the Arnold Arboretum.

FIGS. 1–12. CHROMOSOMES OF VIBURNUM. 1, *V. fragrans* var. *candidissima*, metaphase II; 2, *V. carlesii*, late metaphase I; 3, *V. ovatifolium*, metaphase I; 4, *V. rhytidophylloides*, telophase II; 5, *V. pubescens*, metaphase I; 6, *V. veitchii*, metaphase I; 7, *V. plicatum*, metaphase I; 8, *V. plicatum* f. *mariesii*, metaphase I; 9, *V. dilatatum* f. *hispidum*, metaphase II; 10, *V. dentatum*, metaphase I; 11, *V. dilatatum* f. *xanthocarpum*, metaphase II; 12, *V. opulus* f. *xanthocarpum*, metaphase I. Each division in the scale represents 10 micra.



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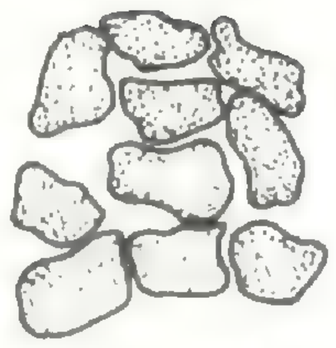

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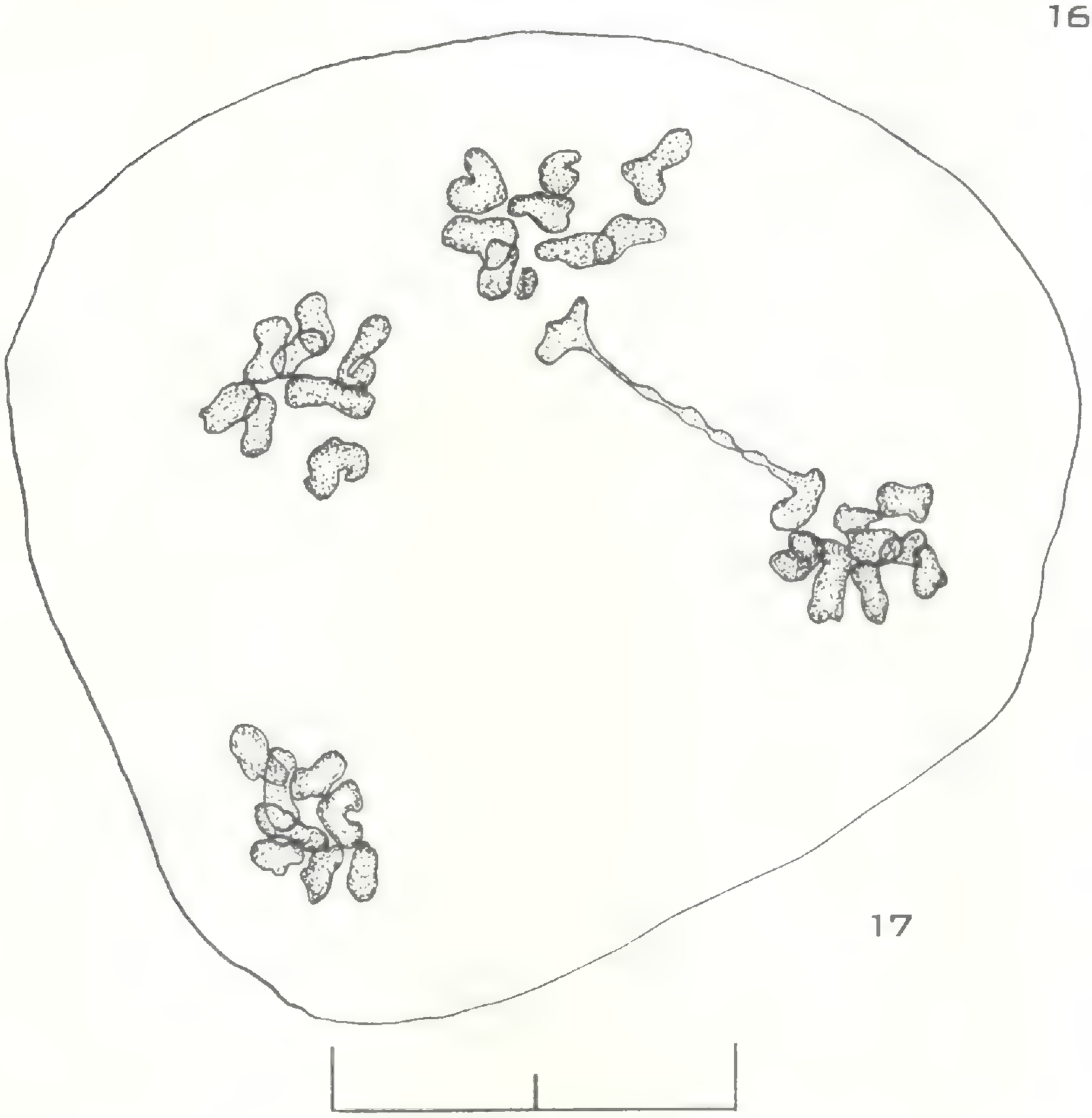

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FIGS. 13–17. CHROMOSOMES OF VIBURNUM. 13, *V. cassinoides*, metaphase I; 14, *V. urceolatum*, metaphase I; 15, *V. rafinesquianum* var. *affine*, metaphase I; 16, *V. lantana* var. *rugosum*, metaphase II; 17, *V. rhytidophylloides*, telophase II, showing loss of a chromosome due to unequal translocation. Each division in the scale represents 10 micra.

slide, immersing the slide in Carnoy's fixative for ten to twenty minutes, and staining the material with acetocarmine. In a few cases, counts were made on root tips obtained from rooted cuttings. The root tips were treated for two to three hours in 0.1% colchicine, fixed in Carnoy's solution, softened in concentrated HCl for ten to fifteen minutes, and stained with acetocarmine.

The time of flowering varies considerably in different species of *Viburnum*, and meiosis often occurs over a short period of time. In order to avoid missing meiosis in several species, small cuttings were brought indoors and forced. Most species forced readily after the middle of March and it was much easier to follow their development under the relatively uniform conditions in the laboratory, than under the highly variable spring weather conditions outside.

ORIGIN OF THE ANEUPLOID SERIES

Janaki Ammal (1) has postulated the origin of the chromosome numbers nine and ten starting with a base number of eight for the genus. The number ten was thought to have originated from a backcross between a chance triploid ($2n = 24$) and a diploid ($2n = 16$) to produce $2n = 20$. Plants with this number are referred to as "secondary diploids." The number nine was said to have originated from hybridization between plants having $2n = 20$ and $2n = 16$, and are referred to as "tertiary diploids." The origin of *Viburnum juddii* was cited as an example of the latter.

This explanation is very logical and it is possible that some species of *Viburnum* have originated in this manner. However, in view of the evidence at hand it seems more likely that species with chromosome numbers of eight and ten originated from species with a base number of nine by the gain or loss of a chromosome. The base number nine is by far the dominant number in the Caprifoliaceae, as well as in the genus *Viburnum*. Of the 50 species of *Viburnum* for which chromosome counts are available (not including varieties, forms, or cultivars) twelve have a base number of eight, 33 have nine, and only two have undisputed counts of $x = 10$. Three additional species were reported by some workers to have $x = 10$ but by other workers to have $x = 9$. It seems probable that the discrepancies here are due to real differences in the chromosome numbers of the plants counted, rather than to mistakes in counting. There are no discrepancies reported for species with $x = 8$, whereas three of the five species reported to have $x = 10$ also have reported counts of nine, and one of these also has a count of eleven. Thus, the number ten seems to be relatively unstable, which is what one would expect if it originated by the gain of a chromosome from species with nine. The duplicated chromosome material is apparently lost with little or no deleterious effect on the plant.

Among the species in which there is a discrepancy in the reported chromosome numbers *Viburnum carlesii* is particularly significant. As mentioned above, Janaki Ammal used the case of *V. juddii* to illustrate the origin of the nine-chromosome series. *Viburnum juddii* is an open-

pollinated offspring of *V. carlesii*, with *V. bitchiuense* suggested as the most probable male parent. The chromosome counts reported for these plants by the above author were as follows: *V. carlesii*, $2n = 20$; *V. bitchiuense*, $2n = 16$; and *V. juddii*, $2n = 18$. However, Poucques (2) and Simonet and Miedzyrzecki (6) reported counts of $2n = 18$ for *V. carlesii*, and, upon checking the original plant from which *V. juddii* originated, I found that it, too, has $2n = 18$. It is fortunate, indeed, that the original plant is still growing on the grounds of the Arboretum and that thorough records were kept documenting the female parent of this hybrid species. I have not yet examined the plants of *Viburnum bitchiuense* which are growing in the vicinity of *V. carlesii*, but if they do have a chromosome number of $2n = 16$, as reported, it seems highly unlikely that this species served as the male parent of *V. juddii*.

Chromosome aberrations were fairly common in several of the species of *Viburnum* which I examined, and unequal divisions were noted in several instances. Translocations apparently occurred rather frequently as evidenced by bridge formations observed in several of the species (see FIG. 17). A relatively high percentage of aberrations was noted in *Viburnum cassinoides*, *V. carlcephalum*, *V. carlesii*, *V. dentatum*, *V. plicatum*, *V. rhytidophylloides*, *V. seiboldii*, *V. trilobum* f. *compactum*, and *V. veitchii*.

In a situation such as this the opportunities for gaining or losing a chromosome are greatly increased, and with frequent translocations the chances of losing a chromosome and still retaining a viable chromosome complement are also increased. An example of the gain of a chromosome is that of *Viburnum plicatum* f. *mariesii*, which originated in cultivation. *Viburnum plicatum* and two of its cultivated forms, f. *lanceatum* and f. *roseum* have $2n = 16$, whereas f. *mariesii* has an extra pair of chromosomes which are very small but nevertheless apparently pair and divide normally during meiosis.

Viburnum is still in need of further cytological work to give a more complete picture of the natural distribution of the three chromosome series. Less than half of the species have been studied cytologically, these being cultivated species, for the most part, and, in many cases, species that have been in cultivation for a long time. Additional cytological work, well documented with herbarium specimens, is needed particularly on Asiatic species from the wild.

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MIOCENE FOSSIL WOODS FROM THE COLUMBIA BASALTS OF CENTRAL WASHINGTON

U. Prakash and Elso S. Barghoorn

Over extensive areas of the northwestern United States, especially in Central Washington, there occur thick accumulations of basalt and related pyroclastic sediments. These are known as the Columbia Lava Series and contain within them numerous fossil woods, in places preserved virtually as fossil forests *in situ*. One of the areas most extensively investigated has been designated locally as the Russell Forests, the term proposed by Beck (1945a). The area included under this designation comprises several hundred square miles in an area centered around Vantage, in the Columbia Valley. Beck (1955–1956) noted that in botanical composition and age, the fossil forests are quite comparable in botanical identity, on the generic level, with the well-known leaf impressions from the Latah beds in and around the city of Spokane, Washington. In Beck's extensive studies, he listed (1945a) thirteen localities in which fossil woods had been found in varying abundance.

In a series of informal notes and publications, Beck presented an impressive list of identified fossil dicotyledonous and coniferous woods (Beck 1941a–e; 1942a–c; 1942–43; 1944a–c; 1945a–c; 1948; 1955a–c; 1955–56; 1956). Unfortunately, however, the identifications are, with few exceptions, not associated with illustration, anatomical description and formal binomial designation. Hence, they do not constitute permanent accessible additions to palaeobotanical and palaeogeographic literature. The authors are in full agreement with the validity and accuracy of Beck's investigations on the fossil woods of central Washington and wish to dedicate this study, in part, to commemoration and formalization of his many years of painstaking work in this difficult aspect of palaeobotanical research. The genera and species described in this paper comprise only a fraction of those which have been determined from the Columbia Basalt fossil forests, and it is proposed to expand our taxonomic treatment of this flora as additional material is examined.

The locality of particular interest is near the town of Vantage, Kittitas County, Washington, on the west bank of the Columbia River about 28 miles east of Ellensburg. From Beck's study (1945a) and our own observations, it is evident that the Vantage locality is rich in quantity and diversity of fossil woods. It is of much interest also to note that this region, once covered by a rich deciduous forest, is now featured by a semiarid sagebrush vegetation (*Artemisia*). The various causes for extinction of the forest, the pronounced changes in climate and topography of the region and other related problems will be dealt with in a subsequent paper when the flora and its ecological significance are more fully known.

This paper deals with the systematic description of woods belonging to the families Aceraceae, Ebenaceae, Fagaceae, Hamamelidaceae, Juglandaceae, Leguminosae, Platanaceae, and Ulmaceae. The field collection was made in 1954 by Mr. Jay O'Leary while he was a student in Harvard College. Our determinations are based on his specimens and preparations supplemented by additional thin-sections.

In general, the preservation of structural details of the wood is quite good, although not consistently so. The siliceous matrix fluctuates from hyaline to microcrystalline but is not accompanied, to any serious degree, by opaque minerals. Some specimens are varicolored by iron mineral stain, but even in these cases the woody structure is well preserved.

The age of the fossil woods described in this study is Upper Miocene. This determination is consistent with the presently accepted stratigraphic position of the Columbia basalts in this area of Washington.

ACERACEAE

1. **Acer puratanum** Prakash & Barghoorn, sp. nov. (FIGS. 25–28, 30)

Growth rings: Fairly distinct (FIG. 27), delimited by 2 or 3 rows of thick-walled fibers.

Vessels: Small, 30–72μ in tangential diameter (mean 53μ); chiefly solitary (FIG. 27), often in multiples of 2–several cells, quite uniform in size and evenly distributed, thin-walled, the solitary vessels round to oval in cross-section. Vessel elements 130–350μ long, with spiral thickenings (FIG. 26). Perforation plates exclusively simple, oblique, often tailed. Intervascular pit-pairs bordered (FIG. 30), alternate, orbicular or angular where crowded, 5–7μ in diameter, with linear apertures. Tyloses absent; vessels often plugged with yellow or brown gummy deposits.

Parenchyma: Sparse, restricted to occasional cells; terminal and paratracheal. Terminal parenchyma occurring as scattered cells associated with the narrow terminal bands of thick-walled fibers. Paratracheal parenchyma (FIG. 25) scanty, occurring as a few cells in association with the vessels. Parenchyma cells sometimes crystalliferous.

Xylem rays: Homogeneous (Kribs Homogeneous Type 1), composed chiefly of procumbent cells (FIG. 28), nonstoried, 1–5 cells wide; uniseriate rays quite common, 1–15 (often 3–8) cells high; multiseriate rays mostly 3–4 cells broad and 0.56 mm. high; up to 8–12 rays per mm. Ray cells square, rectangular or oval in tangential section, thin- to moderately thick-walled and 10–20μ in diameter.

Imperforate tracheary elements: Fiber tracheids (FIG. 25) thin- to moderately thick-walled, especially through the late-wood zone near the growth ring, usually polygonal in cross-section with a small to large lumen, 8–20μ in diameter, nonseptate; pits bordered.

MATERIAL. A single specimen of silicified, mature, secondary xylem measuring 4 × 4 × 3 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55200. The name is derived from Sanskrit, *puratan*, meaning *ancient*.

There is close agreement in almost all details of structure of this wood with that of *Acer*. The fossil wood shows also a superficial resemblance to the mature secondary xylem of *Betula* as seen in transverse and tangential sections. However, in *Betula*, the perforation plates are scalariform, in contrast with the simple plates in *Acer*. Also, spiral thickenings are present in the vessels of *Acer* but absent in *Betula*. A survey of available woods of *Acer* indicates that the nearest affinity of the fossil within this genus is with *A. circinatum* Pursh and *A. mandschuricum* Maxim., especially with the former. Our survey included the study of thin-sections of the woods of 29 species of the genus and published descriptions of 14 other species. The latter are *A. oblongum* Wall., *A. caesium* Wall., *A. thomsonii* Miq. (Pearson and Brown, 1932, pp. 299–308, *figs. 107–111*), *A. pseudoplatanus* L. (Kribs, 1959, *fig. 61*), *A. cissifolium* C. Koch., *A. rufinerve* Sieb. & Zucc. (Kanehira, 1921a, pp. 17, 18), *A. rubescens* Hay., *A. kawakamii* Koidz., *A. duplicato-serratum* Hay., *A. oliverianum* Pax var. *nakaharai* Hay., *A. taiton-montanum* Hay., *A. morrisonense* Hay. (Kanehira, 1921b, pp. 74–76, *pl. 14, figs. 79–81*), *Acer circinatum* Pursh, and *A. leucoderme* Small (Stark, 1954, pp. 8, 10).

The size and distribution of the vessels in *Acer puratanum* agree with the distributional pattern in *A. circinatum*. Tangential diameter of vessels in *A. puratanum* (30–72μ) is quite comparable to the measurements secured from comparable secondary xylem of *A. circinatum* (25–72μ). Both in *A. circinatum* and in the fossil species the perforations are simple and the intervascular pit-pairs are alternate, bordered, orbicular, or angular where crowded, with linear apertures. However, the vessels are more closely placed in the fossil wood than in the modern wood of *A. circinatum*.

The distribution of parenchyma appears to be almost identical in both, as is the fiber and ray structure. However, conspicuous differences between the two species are in the crystalliferous parenchyma and the distribution of thick-walled fibers. The crystalliferous parenchyma is occasionally present in the fossil wood but absent in *Acer circinatum*, although it is known to occur in a number of other species of *Acer*. Also, *A. circinatum* shows alternate areas of thin- and thick-walled fibers (Stark, 1954, p. 8), whereas in *A. puratanum* thick-walled fibers are found only in the late wood.

Fossil woods related to *Acer* are known from the Cretaceous onward under the names *Acerinum* Unger (1842), *Aceroxylon* Loubière (1939), and *Acer* L. These woods are *Acerinum danubiale* Unger (1842), from the Tertiary of Upper Austria; *A. borussicum* Caspary (1888) and *A. terraecoeruleae* Caspary (1888), from the Tertiary (?) of East Prussia; *A. aegypticum* Schenk (1888, 1890), from the Tertiary of Egypt; *A. astianum* Pampaloni (1904), from the Tertiary of the Piedmont; *Aceroxylon madagascariense*, from the Cretaceous of Madagascar (Loubière, 1939); *Aceroxylon* cf. *paleosaccharinum* Greguss (1943), from Hungary; *Aceroxylon* sp., from the Oligocene of Prambachkirchen, Austria (Hofmann, 1944, 1952); *Acer* sp. (Szafer, 1914; Fietz, 1926b), from the Pleistocene of Poland, and from the prehistoric deposits of Czechoslovakia; *Acer iwatense*

Watari (1941, 1952) and *Acer* cf. *amoenum* Carr. (Watari, 1952), from the Tertiary of Japan. However, our present fossil wood differs distinctly from all the known species. Thus, *Acer* cf. *amoenum* (Watari, 1952) differs from *A. puratanum* in having broad xylem rays 1–9 cells wide and in the presence of diffuse parenchyma in addition to paratracheal and terminal types. Diffuse parenchyma is absent from *A. puratanum*. Similarly, *A. iwatense* (Watari, 1941, 1952) also differs from *A. puratanum* in having broad, homogeneous to heterogeneous xylem rays, 1–7 cells wide, and in the presence of only diffuse parenchyma.

The family Aceraceae is composed of two genera and about 150 species. One genus, *Dipteronia*, comprises two species of small trees indigenous to China. The other, *Acer*, composed of numerous species of small to large deciduous trees, is widely distributed over the Northern Hemisphere, one form extending south of the equator to the mountains of Java. It attains its greatest development in eastern Asia and eastern North America (Record and Hess, 1943; Stark, 1954). There are only thirteen species of *Acer* indigenous to the United States. *Acer saccharum* Marsh. and *A. nigrum* Michx. occur in most of the eastern hardwood region of the United States and Canada and also locally in northeastern South Dakota, with the best stands near the Great Lakes and in northern New England and the St. Lawrence Valley (Munns, 1938, *maps 148, 149*; Record and Hess, 1943). *Acer saccharum* Marsh. also grows in southwestern Manitoba, eastern Oklahoma and northeastern Texas. The two principal soft maples, *A. rubrum* L. and *A. saccharinum* L., have much the same range, but extend farther south and attain their best development in the lowlands of the Ohio Valley (Munns, 1938, *maps 150, 151*). *Acer macrophyllum* Pursh grows along the Pacific Coast, from British Columbia to southern California, with the greatest development in Washington and Oregon (Munns, 1938, *map 147*). *Acer pennsylvanicum* L. (Munns, 1938, *map 146*) and *A. spicatum* Lam. grow in the undergrowth of the northeastern hardwood forests and also south in the mountains to northern Georgia (Record and Hess, 1943). *Acer circinatum* Pursh grows naturally along streams and lakes, often forming impenetrable thickets, from British Columbia to northern California, mainly near the coast (Britton, 1908, p. 642). *Acer negundo* L. ranges naturally from western Vermont to western New Jersey and central Florida, westward to Ontario, Manitoba, central Saskatchewan, southern Alberta, central Montana, Wyoming, Utah, California, and Mexico (Munns, 1938, *map 152*; Little, 1953). *Acer leucoderme* Small inhabits rocky river-banks and ravines from North Carolina and Georgia, westward to southeastern Oklahoma and Louisiana. *Acer grandidentatum* Nutt. is a species of the Rocky Mountain region and ranges from northern Montana to eastern Utah, Wyoming, western Texas, and New Mexico, extending southward into Mexico. *Acer barbatum* Michx. (*A. floridanum* (Chapm.) Pax) grows naturally from southeastern Virginia to central Florida and is reported to exist farther west in Texas, northern Mexico, and north in the Mississippi Valley to southeastern Missouri. *Acer glabrum* Torrey grows from Montana, southwestern Oregon, and Idaho to Wyoming,

western Nebraska, and throughout Colorado to New Mexico and Arizona, and also the Sierra Nevada of California (Britton, 1908, pp. 640–56; Little, 1953).

2. **Acer beckianum** Prakash & Barghoorn, sp. nov. (Figs. 59–63)

Growth rings: Distinct, delimited by 1 or 2 layers of flattened thick-walled fibers.

Vessels: Small, 30.6–81.5μ in tangential diameter (mean diameter 60μ), chiefly solitary (Fig. 62), sometimes in multiples of 2 or 3 or rarely 4 or 5 cells, uniform in size and evenly distributed, slightly thick-walled, the solitary vessels round to oval in cross-section (Figs 61, 62). Vessel segments 102–408μ long with spiral thickenings (Fig. 59); end walls usually oblique, sometimes horizontal and often tailed. Perforation plates exclusively simple. Intervascular pit-pairs (Fig. 60) bordered, alternate, 7–8μ in diameter, orbicular (or angular where crowded) with linear apertures. Tyloses absent; vessels sometimes plugged with brown or black gummy deposits.

Parenchyma: Sparse, terminal and paratracheal. Terminal parenchyma scanty, associated with the growth ring. Paratracheal parenchyma found as 1–few cells in association with some vessels.

Xylem rays: Homogeneous (Kribs Homogeneous Type 1) composed chiefly of procumbent cells, nonstoried; 1–3 cells wide; uniseriate rays quite frequent, 3–16 cells high; multiseriate rays mostly 3 cells broad and 0.7 mm high; up to 12–16 rays per mm. Ray cells round to oval, sometimes vertically elongate in tangential section, thick-walled and 7–14μ in diameter.

Imperforate tracheary elements: Fiber tracheids polygonal in cross-section, 10–18μ in diameter, the walls thin to thick, with a small to large lumen, non-septate; pits bordered.

Material. A single specimen of silicified, mature, secondary xylem measuring 4 $\times$ 2.5 $\times$ 3 cm.

Holotype. Palaeobotanical Collections, Harvard University, No. 55226. The species is named in honor of George F. Beck, of Yakima, Washington, who pioneered the work on the fossil woods of Vantage and its neighboring areas.

A survey of all available woods of the genus *Acer* indicates that the nearest affinity of the fossil is with *Acer negundo* L. The size and distribution of the vessels of *A. beckianum* agree with the distributional pattern in *A. negundo* var. *violaceum* Jaeg. & Beissn. The tangential diameter of the vessels in the fossil wood (30.6–81.5μ) is somewhat similar to the measurements secured from comparable secondary xylem of *A. negundo* (25–80μ). The only obvious difference between the two species is in the shape of the vessels which are mostly oval and slightly angular in *A. negundo* but almost always round in *A. beckianum*.

The distribution of parenchyma appears to be almost identical in both,

as is the fiber and ray structure. However, a minor difference between the two species is in lower and rarely 4-seriate rays in *A. negundo*; the rays are slightly higher and up to 3-seriate in *A. beckianum*.

As previously noted, a number of fossil woods related to *Acer* are known and all of them differ from *Acer beckianum* in certain features. The fossil wood of *A. puratanum* Prakash & Barghoorn, described in the preceding pages and from the same locality, also differs distinctly from *A. beckianum*.

3. **Acer olearyi** Prakash & Barghoorn, sp. nov. (FIGS. 55–58)

Growth rings: Slightly distinct, delineated by flattened, thick-walled fibers.

Vessels: Small, 30–80μ in tangential diameter (FIG. 55), (mean diameter 58.5μ); commonly in multiples of 2–8 cells, often solitary, almost uniform in size and evenly distributed, thin-walled, the solitary vessels round to oval or slightly angular in cross-section, radially compressed when in multiples. Vessel elements with spiral thickenings, the end walls probably oblique. Perforation plates exclusively simple. Intervascular pit-pairs bordered, alternate, slightly loosely arranged, 5–7μ in diameter, orbicular (or angular when crowded), with linear to lenticular apertures. Tyloses absent, but vessels commonly plugged with brown or black gummy deposits (FIG. 55).

Parenchyma: Scanty, terminal, paratracheal and diffuse. Terminal parenchyma occurs as occasional cells associated with the rows of thick-walled fibers at the growth ring. Paratracheal parenchyma very sparse, 1–few cells associated with the vessels, sometimes forming incomplete sheaths.

Xylem rays: Homogeneous (Kribs Homogeneous Type 1), composed of procumbent cells (FIG. 58), nonstoried, 1–7 cells wide; uniseriate rays common, 3–16 cells high; multiseriate rays mostly 5 or 6 cells broad and 1.05 mm. high; up to 8–10 rays per mm. Ray cells square, rectangular, or polygonal in tangential section and 8–15μ in diameter.

Imperforate tracheary elements: Fiber tracheids oval to angular in cross-section, 12–25μ in diameter, the wall thin to thick with a small to large lumen, non-septate; pits bordered.

MATERIAL. A single specimen of silicified, mature, secondary xylem measuring 3.5 $\times$ 4 $\times$ 2.5 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University No. 55311. This species is named for Mr. Jay O'Leary, who collected this material.

A survey of all available woods of the genus *Acer* indicates that the nearest affinity of the fossil is with *Acer grandidentatum* Nutt. Both in *Acer olearyi* and the modern wood of *A. grandidentatum* the vessel size and their distribution, the nature of the perforation plates, the intervascular pit-pairs, the parenchyma distribution, and the ray and fiber structure are similar. However, the only obvious difference between the two species is that the vessels are more crowded and with a slightly greater frequency of the vessel multiples in *A. grandidentatum* than in *A. olearyi*.

Acer grandidentatum Nutt. occurs in the western United States and ranges from northern Montana to eastern Utah, Wyoming, western Texas, and New Mexico, extending southward into Mexico (Britton, 1908, p. 652). The present fossil wood differs from all extant species examined as well as from the other fossil species described so far.

EBENACEAE

4. **Diospyros washingtoniana** Prakash & Barghoorn, sp. nov.

(FIGS. 46–50)

Growth rings: Distinct; wood semi-ring-porous (FIG. 47).

Vessels: Large vessels in the early wood, gradually decreasing in size towards the outer margin of the ring (FIG. 47), 40–240μ in tangential diameter (mean diameter 146μ); sometimes solitary, usually in radial rows of 2–4 cells, evenly distributed and somewhat widely placed, thick-walled; solitary vessels round to oval or elliptical in cross-section (FIGS. 47, 49), sometimes irregular in shape. Vessel elements 190–310μ long with horizontal to oblique end walls. Perforation plates exclusively simple. Intervascular pit-pairs bordered, minute, 3–5μ in diameter, orbicular to oval, with linear apertures, sometimes confluent. Vessels often plugged with black or brownish gummy deposits and tyloses (FIG. 50).

Parenchyma: Paratracheal, metatracheal, and terminal. Paratracheal parenchyma confined to immediate vicinity of the vessels, the sheath being narrow, 1- or 2-seriate but incomplete. Metatracheal parenchyma distinguishable with difficulty in cross-section because of bad preservation, but apparently quite abundant and arranged in broken, irregular tangential bands 1–3 cells thick, sometimes ending blindly. Terminal parenchyma forming a 1- or 2-seriate tangential band at the growth ring. Parenchyma cells usually larger than the fibers, variously shaped, those occurring in close association with the vessels flattened to conform to the vessel wall, those found elsewhere oval to rectangular in shape.

Xylem rays: Homogeneous to heterogeneous, storied (FIG. 48) but slightly irregular in some places, 1–2(mostly 2)-seriate and 0.45 mm. high; uniseriate rays 2–13 cells high; biseriate rays up to 18 cells high. Ray cells thick-walled, broadly oval to vertically elongate in tangential section, 10–20μ in diameter.

Imperforate tracheary elements: Slightly thick-walled fiber tracheids variously shaped, more or less angled in cross-section, 20–35μ in diameter, non-septate; pits bordered, with slit-like vertical apertures.

MATERIAL. A single specimen of mature secondary xylem, measuring 9 $\times$ 6 $\times$ 5 cm. Structural preservation of the fossil wood is poor.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55305.

The affinity of the fossil wood is clearly with the genus *Diospyros*, although it shows a superficial resemblance to the mature secondary xylem of *Carya*. The broad rays of *Carya*, however, are nonstoried, whereas the fossil possesses conspicuously storied, narrow rays.

A survey of all of the available woods of the genus *Diospyros* indicates that the nearest affinity of the fossil is with *D. virginiana* L. Our survey included the study of thin sections of woods of 19 species of the genus and published descriptions of 15 other species (Kanehira, 1921a, pp. 38, 39, *fig. 26*; 1921b, pp. 141–144, *pl. 27*, *fig. 160*; 1924, pp. 41, 42; Pearson and Brown, 1932, pp. 698, 699, 706–708, *figs. 226*, *229*; Reyes, 1938, pp. 408–412, 414–415, *pl. 79*, *fig. 3*, *pl. 80*, *figs. 1–3*; Kribs, 1959, pp. 38, 39, *figs. 129*, *358*, *359*).

The size and distribution of the vessels of *Diospyros washingtoniana* agree with the distribution pattern in *D. virginiana*. The tangential diameter of the vessels in the fossil wood (40–240μ) is quite close to the measurements secured from comparable secondary xylem of *D. virginiana* (35–220μ). The only obvious difference between the two species is in slightly more thickened vessel walls in *D. virginiana* which also shows vessel groups up to 7 cells. However, both in *D. virginiana* and in the fossil species, the perforations are simple and the intervascular pit-pairs are bordered, alternate, orbicular to oval with linear aperture.

The distribution of parenchyma appears to be almost identical in both as is also the fiber structure.

The xylem rays of the fossil wood and of *Diospyros virginiana* are basically similar, although there are slight differences. In both they are homogeneous to heterogeneous and storied, although the storied structure is slightly irregular in certain areas of the fossil. The rays of *D. virginiana* are 1–3 (mostly 1 or 2) cells broad, often with long, uniseriate wings, whereas in *D. washingtoniana* they are 1 or 2 (mostly 2) cells broad with short uniseriate wings.

Only two other fossil woods of *Diospyros* are known. These are *Diospyros* sp. (Schonfeld, 1925), from the Tertiary of Germany, and *Diospyros* sp. (Slijper, 1932), from the Pliocene of Holland. It is interesting to note that a fossil wood, *Ebenoxylon speciosum*, showing resemblance to *Diospyros* is also known from the Tertiary of California (Platen, 1908).

The genus *Diospyros* is composed of 160 or more species, mostly trees, more abundant in tropical Asia than elsewhere. *Diospyros virginiana* L. is the only representative in temperate North America. It grows in forests, primarily on dry soil, from Rhode Island to southern New York, Iowa, Kansas, Florida, and Texas (Britton, 1908; Munns, 1938, *map 162*).

FAGACEAE

5. **Quercus leuca** Prakash & Barghoorn, sp. nov. (FIGS. 39–45)

Growth rings: Distinct; wood ring-porous. Transition between early and late wood abrupt.

Vessels: Large vessels in the early wood, 130–390μ in tangential diameter (mean 252μ) (FIGS. 43, 45), solitary, forming a conspicuous band 1–2 pores in width, thin-walled, vessels round to oval in cross-section. Vessel elements up to 400μ long. Perforation plates exclusively simple, usually horizontal. Intervascular pit-pairs alternate, bordered, and round to oval

in shape. Tyloses common. Late-wood vessels small (FIG. 45), 25–75μ in tangential diameter (mean 47μ), scattered in radially aligned, flame-shaped tracts (FIGS. 43, 45) of light-colored tissue, usually solitary, sometimes in pairs, rarely in threes, open, angular in cross-section. Perforation plates and intervascular pit-pairs similar to early-wood vessels.

Parenchyma: Abundant, paratracheal and metatracheal. Paratracheal parenchyma intermingled with the tracheids, (1) forming part of the conjunctive tissue between the early wood vessels and the rays, (2) comprising most of the tissue in the flame-shaped tracts (FIG. 41) in which late-wood vessels are inserted. Metatracheal parenchyma scanty (FIG. 42), restricted to fibrous tracts, mostly in the outer half of the growth ring where it occurs as diffuse, isolated cells or in broken, wavering lines 1 or 2 cells (mostly 1) thick. Parenchyma cells thin walled (FIG. 42), slightly larger than the fiber, very often containing brownish, gummy deposits. Crystalliferous parenchyma abundant, cells slightly swollen (FIG. 39) with rectangular to polygonal crystals.

Xylem rays: Homogeneous (Kribs Homogeneous Type 1), composed of procumbent cells; both narrow and aggregate (FIG. 44); narrow rays mostly uniseriate, rarely partly biseriate, 2–29 cells high; aggregate rays 18–35 cells broad and 14.5 mm. high. Ray cells thin-walled, variously shaped in tangential section and 7–25μ in diameter, sometimes with crystals in swollen elements.

Imperforate tracheary elements: Libriform fibers and vasicentric tracheids. Thick-walled fibers well developed between the spaces among the flame-shaped tracts, polygonal in cross-section, 12–20μ in diameter, non-septate; pits simple. Vasicentric tracheids intermingled with parenchyma, (1) forming most of the conjunctive tissue between the early-wood vessels and the rays and, (2) comprising part of the flame-shaped tracts in which the late-wood vessels are distributed; pits bordered, round and in 1 or 2 rows, aperture round to elliptic (FIG. 40).

MATERIAL. A single specimen of silicified mature secondary xylem measuring 7.5 × 2.5 × 13 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 54916.

The woods of the various species of oaks exhibit considerable variation but possess many features in common. Anatomically, two groups of species can be readily distinguished, the white oak group and the red-black oak group (Record and Hess, 1943, p. 168). These divisions correspond to important botanical differences. The woods can also be grouped into ring-porous, from deciduous trees, and diffuse-porous, from the evergreen or so-called live oaks, but these distinctions are not taxonomic. The red oaks can be distinguished from the white oaks by the following anatomical characters (Brown, Panshin, and Forsaith, 1949, p. 544):

WHITE OAKS	RED OAKS
Transition from early to late wood generally abrupt.	Transition from early to late wood gradual to more or less abrupt.

WHITE OAKS	RED OAKS
Early-wood pores in the heart-wood usually occluded with tyloses.	Early-wood pores in the heart-wood usually open.
Late-wood pores thin-walled, more or less angular, not sharply defined with a hand lens.	Late-wood pores plainly visible with a hand lens, thick-walled, rounded.
Large rays averaging 1/2–1 1/4″ in height, frequently taller than 1 1/2″.	Large rays averaging 1/4–1/2″ in height, rarely taller than 1 1/2″.

According to these characters, the fossil wood under consideration belongs to the white oak group. A survey of the available woods of the genus *Quercus* indicates that the nearest affinity of the fossil is with *Quercus alba* L. Our survey included the study of thin-sections of the woods of 86 species of the genus and published descriptions of 15 other species (Sudworth and Mell, 1911, pp. *22–56*, *figs. 11–48*; Kanehira, 1921a, pp. 67–71, *pl. 8*, *figs. 44*, *45*; Kanehira, 1924, p. 52; Kanehira, 1940; Pearson and Brown, 1932, pp. 981–996, *figs. 299–304*; Reyes, 1938, pp. 60–62, *pl. 4*, *figs. 1*, *2*; Metcalfe and Chalk, 1950, pp. 1311–1314, *figs. 313G*, *L*; Greguss, 1947, pp. 41–46, *figs. 18–27*).

The size and distribution pattern of the vessels in early and late wood of *Quercus leuca* and *Q. alba* are almost identical, there being 1 or 2 rows of large vessels in the early wood and small, thin-walled, angular vessels arranged in a flame-like pattern in the late wood. In addition, both in the living and fossil species the perforation plates are exclusively simple and the intervascular pit-pairs are bordered, alternate, and round to oval.

The distribution of parenchyma appears to be almost identical in both, as is the fiber structure. However, a conspicuous difference between the two species is in the crystalliferous parenchyma, which is present in the fossil wood but absent in *Quercus alba*.

The xylem rays of the fossil wood and of *Quercus alba* are basically similar, although there are slight differences in the height of the rays and in the presence of crystals in the ray cells of the fossil. In both they are narrow (mostly uniseriate) and aggregate and composed solely of procumbent cells. However, the rays are 14.5 mm. high and possess large crystalliferous cells in *Q. leuca*, whereas in *Q. alba* they are much higher and do not have crystalliferous cells.

Fossil woods and leaves assigned to *Quercus* are known from the Cretaceous onward from many areas of the earth. Fossil woods have been described under the names *Quercinium* Unger (1842, emend. Brett, 1960), *Quercoxylon* Krausel (1939) and *Quercus* L. These have been listed by Edwards (1931) and Boeshore and Jump (1938). Others not listed and subsequently described are by Ogura (1932), Shimakura (1934), Krausel (1939), Watari (1941, 1952), Hofmann (1944, 1952), Andreanszky (1951), Beyer (1954), Müller-Stöll & Mädel (1957), Boureau (1958), and Brett (1960). All of them differ distinctly from the fossil wood under consideration. Those known from this country are *Quercinium knowltonii* Felix (1896), *Q. lamarense* Knowlton (1899), *Quercus rubida* Beyer

(1954), from the Miocene of Yellowstone National Park; *Quercinium album* Boeshore & Jump (1938), from the Miocene of Idaho; *Quercinium solerederi* Platen, *Q. wardii* Platen, *Q. anomalum* Platen, *Q. lesquereuxii* Platen, *Q. abromeitii* Platen (Platen, 1908), and *Quercus ricardensis* Webber (1933), from the Miocene and Pliocene, and *Q. agrifolia* Nee (Frost, 1927), from the Pleistocene of California; and *Quercus marcayana* Penhallow (1891), from the post-glacial deposits of Illinois.

Quercus, one of the most important woody genera in the world, is widely distributed in the North Temperate Zone and extends at high altitudes into the tropics as far south as the East Indies in the Old World and the mountains of Colombia and Ecuador in the New World. More than 500 species and varieties of oaks, from low shrubs to stately forest trees, have been described (Record and Hess, 1943).

There are about fifty species of *Quercus* native to the United States. *Quercus alba* L., with which our fossil compares well, grows throughout the entire eastern half of the United States (Munns, 1938, *map 110*). The only oak growing in the state of Washington is *Q. garryana* Douglas (Record and Hess, 1943; Munns, 1938, *map 112*) which also belongs to the white oak group.

HAMAMELIDACEAE

6. **Liquidambar** cf. **styraciflua** L. (FIGS. 20–24)

Growth rings: Not very conspicuous, delimited by 1 or 2 rows of thick-walled, flattened fibers; wood diffuse-porous (FIG. 20).

Vessels: Small, 30–81μ in tangential diameter (mean 48μ), solitary, in multiples of 2 or 3 (mostly 2), or paired laterally, quite uniform in size and crowded (FIG. 20), thin-walled, oval to slightly angular in cross-section. Vessel elements up to 1070μ long, with tapering, often tailed ends; spiral thickening present, restricted to tapering ends. Perforation plates exclusively scalariform with about 15–30 bars (FIG. 22). Intervascular pit-pairs (FIG. 23) bordered, in transverse rows of 1–3, orbicular to oval or linear through fusion, 7–35μ in diameter. Tyloses absent.

Parenchyma: Scanty, paratracheal and diffuse, either associated with the vessels or found as solitary cells among the fibers; parenchyma cells thin-walled, oval to oblong in cross-section.

Xylem rays: Heterogeneous, nonstoried, 1–3 cells wide; uniseriate rays 5–18 cells high, composed of both upright and procumbent cells; multiseriate rays 2 or 3 (mostly 3) cells broad through the central portion of procumbent cells, with uniseriate extensions above and/or below composed wholly or mainly of upright cells; sometimes with end to end ray fusion; up to 12–20 rays per mm.

Imperforate tracheary elements: Fiber tracheids quadrangular to polygonal in cross-section, 15–35μ in diameter, the walls fairly thick (FIG. 24), non-septate; pits bordered, with vertical or oblique, linear apertures.

MATERIAL. A single specimen of silicified mature secondary xylem

measuring 2 × 2.5 × 8 cm. Structural preservation of the fossil wood poor.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55240.

The fossil wood shows a superficial resemblance to the mature, secondary xylem of *Cercidiphyllum*. However, *Cercidiphyllum* differs from the present fossil wood in having 1- or 2-seriate heterogeneous rays with very frequent end-to-end ray fusion and in having numerous (20–50) bars in the perforation plates.

A survey of all available woods of the *Liquidambar* indicates that the nearest affinity of the fossil is with *Liquidambar styraciflua* L. Our survey included the study of thin-sections of the woods of *L. styraciflua* L., and *L. formosana* Hance.

The size and distribution of the vessels of the fossil wood under consideration agree with the distribution pattern in *Liquidambar styraciflua*. The tangential diameter of the vessels (30–81μ) in the fossil wood is more or less similar to the measurements secured from comparable secondary xylem of *L. styraciflua*. In both, the perforation plates are scalariform, and the intervascular pit-pairs are in transverse rows of 1–3, orbicular to oval or linear through fusion. The distribution of parenchyma appears to be almost identical in both as is the fiber and ray structure. However, a minor difference between the two is in higher and sometimes 4-seriate rays in *L. styraciflua*.

Only three fossil woods showing resemblance to *Liquidambar* are known. These are *Liquidambaroxylon speciosum* Felix (1884), from the Tertiary of Hungary, *L. lecointreae* Houlbert (1910), from the Middle Miocene of Touraine (Edwards, 1931), and *Liquidambar formosana* Hance (Watari, 1952), from the Pliocene of Yokohama City and the Miocene of Honsyu [Honshu], Japan. These species differ from the present fossil. The fossil wood of *Liquidambar formosana* differs in having mostly scalariform intervessel pits, rays 1–4 (mostly 2–3) cells broad with 2 or 3 rays fused frequently, and in possessing a large number of bars (7–39) in the perforation plates.

Liquidambar is represented by about four extant species, three in eastern Asia and one, *Liquidambar styraciflua* L., in America, where it is commonly known as red or sweet gum. This important timber tree is widely distributed throughout the southeastern part of the United States, its northern and western boundaries being from Connecticut, westward through the Ohio Valley to Kansas, and southward through Oklahoma into Texas. It reappears on the mountains of eastern Mexico and the highlands of southern British Honduras and eastern Guatemala and Honduras. It is most abundant and of largest size in wet, rich soil bordering streams or swamps (Record and Hess, 1943; Britton, 1908; Munns, 1938, *map 131*).

JUGLANDACEAE

7. **Carya tertiara** Prakash & Barghoorn, sp. nov. (FIGS. 14–19)

Growth rings: Distinct, delineated by narrow bands 2 or 3 cells thick,

of flattened, thick-walled fibers; wood semi-ring-porous to diffuse porous. Transition between early and late wood gradual (FIGS. 15, 19).

Vessels: Usually large vessels (FIG. 15) in the early wood, 150–320μ in tangential diameter (mean 214μ), solitary (FIGS. 15, 19) and in radial rows of 2–4 or rarely 5 or 6 cells, thin- to slightly thick-walled, the solitary vessels round to oval in cross-section (FIG. 19). Vessel elements 255–485μ in length with the end walls usually inclined, sometimes truncate, rarely tailed. Perforation plates exclusively simple. Intervascular pit-pairs (FIG. 18) bordered, alternate, orbicular to oval or angular when crowded, 7–12μ in diameter with linear or lenticular apertures. Thin-walled tyloses abundant (FIGS. 15, 17). Late-wood vessels small to medium-sized, 60–150μ in tangential diameter (mean 112.5μ); solitary (FIG. 19) and in radial multiples of 2 or 3 or rarely more; walls thin to conspicuously thickened. Intervascular pit-pairs and perforation plates similar to early wood vessels.

Parenchyma: Paratracheal, metatracheal, metatracheal-diffuse, and terminal. Paratracheal parenchyma varying from isolated cells to uniseriate sheaths partially encircling the vessels. Metatracheal parenchyma (FIGS. 15, 19) in tangential, slightly undulating, usually continuous, sometimes broken, narrow lines 1–3 (usually 1 or 2) cells thick which are arranged irrespective of pores. Diffuse parenchyma scattered among the fibers as groups of two or isolated cells. Terminal parenchyma uniseriate, associated with the flattened fibers at the growth rings. Parenchyma cells thin-walled, oval or tangentially elongate in cross-section, often quite large and crystaliferous (FIGS. 14, 15), 15–40μ in diameter.

Xylem rays: Homogeneous to slightly heterogeneous (FIG. 16), mostly composed of procumbent cells; 1–4 cells wide; uniseriate rays frequent, 2–21 (usually 6–10) cells high; multiseriate rays often fusiform, mostly 3, rarely 4, cells broad and 0.87 mm high with uniseriate wings (up to 11 cells) at one or both ends; broad rays composed either entirely of procumbent cells or rarely with a marginal row of upright cells at one of the ends; up to 9–12 rays per mm. Ray cells 15–30μ in diameter, round to oblong in tangential section, sometimes angular where crowded.

Imperforate tracheary elements: Thick-walled fiber tracheids (FIGS. 15, 19), oval to slightly angular in cross-section, 10–25.5μ in diameter; walls moderately thick with fairly large lumen; non-septate; pits bordered.

MATERIAL. A single specimen of silicified mature secondary xylem measuring approximately 9 $\times$ 7 $\times$ 3 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55210.

There is close agreement in all structural details with the genus *Carya*, except as noted below. A survey of the available woods of the genus *Carya* indicates that the nearest affinity of the fossil is with *C. leiodermis* Sarg. Our survey included the study of thin sections of the woods of 18 species and published descriptions of two additional species. The latter are *C. tonkiensis* Lecomte (Heimsch and Wetmore, 1939, pp. 655–7, *figs. 21, 22*) and *C. texana* var. *arkansana* (Sarg.) Little (Stark, 1953, p. 31).

The fossil wood of *Carya tertiara* resembles the modern wood of *C. leiodermis* in the distribution pattern of the vessels, in the type of perforation plates, in the nature of the intervascular pit-pairs, in parenchyma distribution, and in the nature of the xylem rays. However, *C. leiodermis* differs from the fossil wood under consideration in having slightly narrower (1–3 cells) and higher (1042μ) xylem rays, in possessing fewer tyloses in the vessels, and in having much less crystalliferous parenchyma which is not swollen like that of the fossil wood. On the other hand, swollen crystalliferous parenchyma is seen in the modern woods of *C. pallida* Engl. & Graebn., *C. cordiformis* K. Koch, *C. aquatica* Nutt., *C. tonkiensis* Lecomte, *C. tomentosa* Nutt., *C. illinoensis* (Wang.) K. Koch, *C. glabra* Sweet, and *C. floridana* Sarg. Since the present fossil wood differs slightly from the modern wood of *Carya leiodermis*, it is assigned to a new species, *C. tertiara* Prakash & Barghoorn.

Only two fossil woods of *Carya* are known. These are *Carya* sp. (Beck, 1942a), from the Upper Miocene of Washington, and *C. protojaponica* (Watari, 1952), from the Miocene of Honsyu [Honshu], Japan. Both these species differ quite distinctly from the present fossil wood. Thus *C. protojaponica* differs from *C. tertiara* in having mostly uniseriate, partly biseriate bands of metatracheal parenchyma and in having homogeneous to decidedly heterogeneous xylem rays 1 or 2, rarely 3 or 4, cells broad. However, in *C. tertiara* the metatracheal parenchyma bands are 1–3-seriate and the xylem rays are 1–4 (mostly 1 and 3) cells broad, homogeneous to weakly heterogeneous.

Similarly, the *Carya* species known from Vantage looks different (Beck, 1942a, *pls. 1731e,b,c,k*) from *C. tertiara*. Unfortunately, a detailed comparison between the two is impossible since Beck's material was not illustrated.

Carya includes about 22 species: one is native to China (*C. cathayensis* Sarg.), a second to Indochina (*C. tonkinensis* Lecomte), a third is restricted to the highlands of Mexico (*C. mexicana* Engelm.), and the remaining nineteen are widely distributed in eastern North America. There are also a number of varieties and hybrids (Stark, 1953). *Carya leiodermis* Sarg. grows in northern Florida, western Alabama, Mississippi, southern Arkansas, Louisiana, and eastern Texas (Little, 1953, p. 87). For a detailed distribution of other species, see Munns (1938), Record and Hess (1943), Fernald (1950), and Little (1953).

LEGUMINOSAE

8. **Albizzia vantagiensis** Prakash & Barghoorn, sp. nov. (FIGS. 51–54)

Growth rings: Distinct; wood diffuse-porous (FIG. 52).

Vessels: Large to medium-sized, sometimes small, 76–245μ in tangential diameter (mean diameter 152μ), encircled by a conspicuous halo of parenchyma (FIG. 52), chiefly solitary, sometimes paired, rarely in rows of 3–4 or even 6 cells, thin-walled, the solitary vessels circular to oval in

cross-section. Vessel elements 178–484μ long, with truncate or slightly tailed ends. Perforation plates exclusively simple. Intervascular pit-pairs (FIG. 51) alternate, sometimes slightly opposite, oval to orbicular, and vestured. Tyloses absent, vessels sometimes plugged with gummy deposits.

Parenchyma: Abundant, paratracheal, paratracheal-zonate, terminal, and metatracheal-diffuse. Paratracheal parenchyma (FIG. 54) forms a narrow or wide halo (up to 5 cells thick) about the vessels or vessel groups, frequently extending laterally beyond proximate rays and usually ending blindly or sometimes uniting with those of other vessels forming paratracheal-zonate parenchyma. Terminal parenchyma sparse, forming a 1- or 2(mostly 1)-seriate line at the growth ring. Diffuse parenchyma scanty, cells scattered among the fibers. Parenchyma cells 15–30μ in diameter, occasionally crystalliferous.

Xylem rays: Homogeneous (Kribs Homogeneous Type 2), composed chiefly of procumbent cells (FIG. 53), nonstoried, 1–4 cells wide; uniseriate and biseriate rays rare, the uniseriate rays 5–14 cells high; multiseriate rays mostly 3 cells broad and 0.97 mm. high; up to 6–10 rays per mm. Ray cells thin-walled, circular to oval in tangential section, 10–20μ in diameter.

Imperforate tracheary elements: Libriform to semilibriform fibers polygonal in cross-section, 10–20μ in diameter, walls fairly thick (FIG. 54), with a small to fairly large lumen, nonseptate; pits simple.

MATERIAL. Two specimens of silicified secondary xylem. The type specimen measured 5 × 4 × 5 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55237.

The fossil wood most closely resembles the structural features of the leguminous genus *Albizzia*, although it shows a superficial resemblance to the mature secondary xylem of *Artocarpus* (*A. indica*, *A. chaplasha*), particularly as seen in transverse section. The rays in *Artocarpus*, however, are broad and heterogeneous, whereas the fossil possesses homogeneous, narrow rays. A survey of all available woods of the genus *Albizzia* indicates that the nearest affinity of the fossil is with *A. stipulata* Boivin. Our survey included the study of thin-sections of the woods of 14 species of the genus and published descriptions of 8 other species. The latter are *A. montana* Benth., *A. tomentella* Miq. (Moll & Janssonius, 1914, pp. 193–195), *A. lucida* Benth. (Pearson and Brown, 1932, pp. 465–467, *fig. 158*), *A. acle* (Blanco) Merr. (Kanehira, 1924, p. 25; Kribs, 1959, pp. 63, 64, *fig. 163*), *A. gummifera* C. A. Sm., *A. ferruginea* Benth. (Kribs, 1959, pp. 64, 65, *figs. 397–398*), *A. chinensis* (Osb.) Merr. (Reyes, 1938, pp. 117, 118, *pl. 16, fig. 1*) and *A. retusa* Benth. (Schneider, 1916, pp. 116–118, *pl. 2, fig. 15*).

The fossil wood of *Albizzia vantagiensis* resembles the modern wood of *A. stipulata* in the size and distribution pattern of the vessels, in the perforation plates and intervascular pit-pairs, in parenchyma distribution, and the fiber and ray structure. However, *A. stipulata* differs from the fossil in

having partly septate fibers and slightly wider and very low xylem rays. The rays are 1–5 (mostly 2 or 3) cells broad and 0.23 mm. high in *A. stipulata*, whereas they are 1–4 (mostly 3) cells broad and 0.97 mm. high in *A. vantagiensis*.

Albizzia is a rather large genus of small to large trees widely distributed in tropical Asia, Africa, and America. Of the species the best known is probably *A. lebbek* Benth., native to Asia but planted for shade and ornament throughout tropical regions. *Albizzia julibrissin* Boiv., another Asiatic tree, is widely planted for shade and ornament in the southern United States and has become naturalized in woods and thickets from Virginia to Florida and Louisiana (Britton, 1908, p. 519). Its hardy forma *rosea* (Carr.) Rehd. makes favorable growth under climatic conditions as far north as Boston, Massachusetts.

A large number of fossil woods belonging to the family Leguminosae are known. However, woods related to *Albizzia* are limited to two references in the literature. These are *Leguminoxylon albizziae* Krausel (1939), from the Tertiary of Egypt, and *Albizzioxylon sahnii* Ramunjam (1960), from the Cuddalore series (Mio-Pliocene) of the South Arcot district in South India. *Albizzioxylon sahnii* differs from *Albizzia vantagiensis* in its slightly thickened aliform sheaths of parenchyma around the vessels, its septate fibers, and its short xylem rays (5–15 cells high) locally showing a storied tendency. However, in *A. vantagiensis* the fibers are nonseptate and the rays are quite high (5–55 cells) without any storied arrangement.

9. **Gleditsia columbiana** Prakash & Barghoorn, sp. nov.

(FIGS. 29, 31–34)

Growth ring's: Distinct; wood ring-porous. Transition between the early and late wood quite marked (FIGS. 29, 34).

Vessels: Large vessels in the early wood, 100–214μ in tangential diameter (mean diameter 138μ), chiefly solitary (FIG. 34), occasionally paired, forming a band 4–6 vessels in width, thin-walled, the solitary vessels oval to elliptic in cross-section. Vessel elements 130–265μ long. Perforation plates exclusively simple, usually horizontal, sometimes slightly oblique. Intervascular pit-pairs (FIG. 31) vestured, alternate, orbicular to oval or angular (where crowded), 7–10μ in diameter, apertures linear, often coalescent. Vessels frequently plugged with gum deposits. Late-wood vessels small (FIGS. 29, 34), barely visible with a hand lens, 15–25μ in tangential diameter (mean 21μ), usually in short radial rows or in small groups embedded in short tangential bands of parenchyma; vessels variously shaped, polygonal, irregular, or occasionally oval. Vessel elements with spiral thickenings (FIG. 32). Perforation plates and intervascular pit-pairs similar to early-wood vessels except slightly smaller.

Parenchyma: Quite abundant (FIG. 34), paratracheal, paratracheal-confluent and terminal. Paratracheal parenchyma (1) composing an appreciable portion of the conjunctive tissue between the vessels and the rays in the early-wood zone, (2) forming fairly extensive tracts about vessels

farther out in the ring, and (3) in the late summer-wood extending from the flanks of the vessels and frequently uniting with parenchyma from proximate vessels and forming short, slightly irregular, 4–10-seriate tangential bands of paratracheal-confluent parenchyma in which the vessels or vessel groups are included (FIG. 29). Terminal parenchyma forming a distinct line passing over into the paratracheal parenchyma of the next ring.

Xylem rays: Homogeneous (Kribs Homogeneous Type II) composed of procumbent cells (FIG. 33), 1–5 cells wide; uniseriate and biseriate rays few, the uniseriate rays usually 6–8 cells high; multiseriate rays fusiform, mostly 3–4 cells broad and 0.86 mm. high; up to 6–8 rays per mm. Ray cells slightly thick-walled, orbicular to oval or sometimes angular in tangential section, 8.5–15μ in diameter.

Imperforate tracheary elements: Libriform fibers oval to angular in cross-section, 10–20μ in diameter, the walls moderately thick, with a fairly large lumen, nonseptate; pits simple.

MATERIAL. A single specimen of silicified mature secondary xylem measuring 7 $\times$ 5 $\times$ 8 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55204.

The fossil wood may be assigned to the genus *Gleditsia*, although it also shows resemblance to the mature secondary xylem of *Gymnocladus*. It is rather difficult to distinguish *Gleditsia* from *Gymnocladus* anatomically, but it is proposed to assign the present fossil to *Gleditsia*. However, the possibility remains that it may be the wood of a *Gymnocladus*. Unfortunately, the range of structural variation in the secondary xylem of the fossil is not possible to determine.

Gymnocladus comprises two species, *G. dioicus* (L.) Koch, confined to east-central North America, and *G. chinensis* Baill., known from central China. *Gymnocladus dioicus* differs from the present fossil in having fairly abundant parenchyma forming 1–several(mostly 1)-seriate, occasionally interrupted sheaths about the vessels or vessel groups in the early wood, whereas in the fossil the parenchyma consists of an appreciable portion (usually most) of the conjunctive tissue between the vessels and the rays. Similarly, *G. chinensis* differs from the fossil species in the size and distribution pattern of the vessels in the late-wood zone; in *G. chinensis* they are quite large and usually solitary.

A survey of all available woods of the genus *Gleditsia* indicates that the nearest affinity of the fossil is with *G. triacanthos* L. Our survey included the study of thin-sections of the woods of six species of the genus and published descriptions of two other species. The latter are *G. japonica* Miq. (Kanehira, 1921a, p. 23, *pl. 3, fig. 15*) and *G. formosana* Hay. (Kanehira, 1921b, pp. 93, 94, *pl. 19, fig. 114*).

The size and distribution pattern of the vessels in *Gleditsia columbiana* and *G. triacanthos* (Aw 17464) are almost identical, there being (3)4–6 rows of large vessels (tangential diameter 100–225μ in *G. columbiana*, 125–255μ in *G. triacanthos*) in the early wood and small groups or radial rows

of small vessels (15–25μ in *G. columbiana*, 15–35μ in *G. triacanthos*) embedded in tangential bands of parenchyma in the late wood. In addition, both in *G. triacanthos* and *G. columbiana*, the perforation plates are exclusively simple and the intervascular pit-pairs are alternate, vestured, and orbicular to oval with linear apertures which are often coalescent.

The distribution of parenchyma appears to be almost identical in both, as is the structure of the fibers.

The xylem rays of the fossil wood and of *Gleditsia triacanthos* are basically similar, although there are some differences in the height and breadth of the rays. In both they are homogeneous, composed of procumbent cells of similar size and shape. However, the rays are 1–5 (mostly 3 or 4) cells broad and up to 0.86 mm. high in *G. columbiana*, whereas in *G. triacanthos* they are 1–14 (mostly 6–9) cells broad and the tallest are more than 1.2 mm. high (Brown, Panshin & Forsaith, 1949, *fig. 274*, pp. 576–77). However, in specimen Aw 9454 (Arnold Arboretum wood collections) of *G. triacanthos* examined by us, the rays are only 1–5 (mostly 4 or 5) cells broad but are slightly higher than the present fossil wood.

Only one occurrence of fossil wood of *Gleditsia* (cf. *G. japonica* Miq.), from the Miocene of Japan, is known (Watari, 1952). It differs from the present fossil wood in possessing rays 1–12 cells broad flanked by incomplete sheath cells and in the presence of chambered parenchyma containing solitary crystals.

Gleditsia consists of about eleven species of trees, chiefly Asiatic, usually with the stem and branches heavily armed. It is represented in the Western Hemisphere by only three species, two in eastern North America, the third in southern South America (Record and Hess, 1943). *Gleditsia triacanthos* L. is a large forest tree of scattered occurrence throughout most of the eastern half of the United States, achieving optimum development along small streams in southern Indiana and Illinois (Munns, 1938, *map 142*). *Gleditsia aquatica* Marsh. is a smaller tree of river-swamps, from Florida to Texas, northward to North Carolina, southern Indiana and Illinois, and southeastern Missouri. The single species of the Southern Hemisphere, *G. amorphoides* (Griseb.) Taub., grows in northern Argentina, Bolivia, and southern Brazil.

PLATANACEAE

10. **Platanus americana** Prakash & Barghoorn, sp. nov. (FIGS. 8–13)

Growth rings: Distinct (FIG. 10), marked by a few rows of tangentially flattened fibers.

Vessels: Small (FIG. 10), 30–77μ in tangential diameter (mean diameter 54μ), somewhat smaller in the late summer wood. Vessels solitary and in irregular groups of 2–5 cells, numerous and crowded, and more or less evenly distributed through most of the annual ring (FIG. 10), about 140 per sq. mm. in the early wood, somewhat less abundant and widely spaced in the late summer wood; vessels variously shaped in cross-section (FIG.

10), oval, elliptical, nearly round with sides in contact much flattened, and angular where crowded, those first formed usually compressed tangentially. Vessel elements 305–765μ in length usually with oblique often tailed ends. Perforation plates both simple and scalariform (FIGS 12, 13); simple perforation large, oval to elliptic in shape and more numerous than the scalariform; scalariform perforations uncommon, bars 2–11 in number, fine, widely spaced and occasionally bifurcate (FIG. 12). Intervascular pit-pairs bordered (FIG. 8), opposite to subopposite on the vessel wall, often loosely arranged, oval to orbicular or elongated in shape, 9–12μ in diameter, with slit-like apertures. Tyloses absent. Vessel distribution graded porous (FIG. 10).

Parenchyma: Scanty, paratracheal and metatracheal-diffuse; paratracheal parenchyma restricted to occasional cells never forming a sheath around the vessels; diffuse parenchyma sporadically distributed as isolated cells among the fibers; parenchyma cells oval to elliptic in cross-section.

Xylem rays: Homogeneous (Kribs Homogeneous Type 2), composed of procumbent cells (FIG. 11), 2–15 cells wide; multiseriate rays fusiform (FIG. 11), mostly 6–15 cells broad and 3.84 mm. in height with pointed or blunt ends, often arranged closely and vertically upon each other so as to appear as parts of the same ray dissected into smaller units; up to 3–4 rays per mm. Ray cells thin-walled, oval to oblong (sometimes polygonal) in tangential section.

Imperforate tracheary elements: Thick-walled fiber tracheids with a small lumen, polygonal in cross-section (FIG. 9), 15–25μ in diameter; nonseptate, about 1020μ in length; pits bordered with vertical slit-like aperture.

MATERIAL. A single specimen of silicified mature secondary xylem broken into a number of fragments.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55218.

This fossil wood shows a superficial resemblance to the mature secondary xylem of *Euptelea* and *Fagus*, particularly as seen in transverse section. However, the broad rays of *Euptelea* are conspicuously heterogeneous, whereas the fossil possesses homogeneous multiseriate rays. Similarly, *Fagus* differs from the present fossil wood in having oak-type rays, i.e., large, broad rays accompanied with numerous, small, uniseriate rays.

A survey of all available woods of the genus *Platanus* indicates that the nearest affinity of the fossil within this genus is with *P. wrightii* S. Wats. Our survey included the study of thin sections of the woods of *P. wrightii*, *P. occidentalis* L. and *P. racemosa* Nutt., and published descriptions of three others. The latter are *P. orientalis* L. (Metcalfe and Chalk, 1950, p. 1281, *figs. 300a,b*; Greguss, 1947, pp. 74, 75, *fig. 68*), *P. acerifolia* Willd. (Henderson, 1953, p. 6, *fig. 308*) and *Platanus* sp. (Dadswell and Record, 1936, p. 23, *pl. 2, fig. 3*). The secondary xylem of *P. wrightii* is characterized by small, solitary or irregular groups of 2–5 vessels. There is a conspicuous difference in diameter between the vessels of the early wood and those of the late wood (Brush, 1917, pp. 493, 494, *pl. 33*). The

size and distribution of the vessels in *P. americana* agree with the distribution pattern in the modern *P. wrightii*. Mean tangential diameter of vessels in *P. americana* (54μ) is quite comparable to the measurements secured from comparable secondary xylem of *P. wrightii* (61μ). In both *P. wrightii* and the fossil species the intervascular pit-pairs are bordered, oval to elongate, usually opposite, sometimes alternate, and often loosely arranged in vertical rows. Similarly, simple as well as scalariform perforations are present in both *P. wrightii* and the fossil species. However, in *P. wrightii* the scalariform perforations are more numerous than the simple type and are characterized by 1–20 (most frequently 6–15) closely spaced, fine bars which are sometimes bifurcate. Contrary to this, in *P. americana* simple perforations are more numerous than the scalariform type which are characterized by 2–11 widely spaced bars. It is evident that in this respect the fossil species is more highly specialized than the living species *P. wrightii*. However, in *P. occidentalis*, the perforation plates are simple, for the most part, or occasionally scalariform with a few bars (Brown, Panshin & Forsaith, 1949, p. 570), a condition quite comparable to the fossil wood under consideration.

Very little wood parenchyma is present in the fossil *Platanus* and sometimes it becomes quite difficult, in cross-section, to distinguish parenchyma from the tracheary elements because of the absence of the secondary walls of the latter, which thus resemble parenchyma cells. However, in longitudinal sections it is possible to distinguish between them. The distribution of parenchyma appears to be similar in both, as is the fiber structure; but a conspicuous difference is in the quantity of diffuse parenchyma which is quite abundant in *Platanus wrightii* but much less so in the fossil wood. In *P. wrightii*, parenchyma occurs both as isolated cells and as uniseriate lines of 2–4 or rarely more cells, whereas in *P. americana* it occurs only as diffuse solitary cells.

The xylem rays of the fossil wood and of *Platanus wrightii* are basically similar, although there are slight differences in frequency of broad, multiseriate rays. In both they are very high, usually broad, and homogeneous, composed of round to oval procumbent cells. However, the rays are 2–15 (mostly 6–15) cells broad in *P. americana*, whereas in *P. wrightii* they are 1–14 (rarely uniseriate, mostly 10–14) cells broad.

A number of fossil woods belonging to the family Platanaceae are known from various localities in the world. The woods have been included under the names *Plataninium* Unger (emend. Vater, 1884), *Platanoxylon*, and *Platanus* (Windisch, 1886; Kaiser, 1890; Felix, 1894; Platen, 1908; Schonfeld, 1930; Slijper, 1932; Stockmans, 1936; Hofmann, 1952; Andreánszky, 1951; Beyer, 1954). Those known from this country are *Plataninium crystallophilum* Platen (1908), from the Tertiary of Arizona, *P. pacifica* Platen (1908), from the Miocene of California (Nevada County), *P. knowltonii* Platen (1908), and *Platanus haydenii* (Felix) Beyer (1954), the last two from the Miocene of Amethyst Mountain in the Yellowstone National Park. The general agreement between these and the Vantage fossil wood is close.

The only two fossil woods described under *Platanus* are *Platanus* sp. (Slijper, 1932) and *Platanus haydenii* (Beyer, 1954). Slijper's *Platanus*, from the Pliocene of Reuver, Limburg, Holland, differs from *P. americana* in having spiral thickenings in the vessels and xylem rays 8–10 cells wide (Slijper, 1932, pp. 27, 28, *fig. 3*). Spiral thickenings are not found in the vessels of *P. americana* and the rays are 2–15 (mostly 6–15) cells broad. Similarly, *P. haydenii* (Felix) Beyer, (1954) also differs from *P. americana* in having exclusively simple perforation plates and narrower (3–10-seriate) rays. However, in *P. americana* both simple and scalariform perforation plates are present and the rays are mostly 6–15 cells broad.

Platanus, the only genus of the Platanaceae, includes about eleven species of large trees, three in southern Europe and Asia, eight in temperate North America (Record and Hess, 1943). The largest and the best known species in the United States is *P. occidentalis* L., which is common along streams and lakes and throughout most of the eastern half of North America, growing at optimum in the lower Ohio and Mississippi Valleys (Record and Hess, 1943; Britton, 1908). *Platanus wrightii* S. Wats. and *P. racemosa* Nutt. occur in the southwestern United States and northern Mexico (Record and Hess, 1943; Munns, 1938, *map 132*). Five other species are found only in Mexico.

ULMACEAE

11. **Ulmus miocenica** Prakash & Barghoorn, sp. nov. (Figs. 1–7)

Growth rings: Very distinct; wood ring-porous. Transition between early and late wood quite marked (Figs. 1, 4).

Vessels: Large vessels in the early wood, 81–179μ in tangential diameter (mean 118μ), chiefly solitary, usually arranged in one, sometimes in two rows (Fig. 1), occasionally associated with or interspersed by clusters or radial rows of small vessels (Fig. 4), thick-walled, the solitary vessels circular to oval in cross-section. Vessel elements 153–367μ long. Perforation plates exclusively simple, usually horizontal, sometimes slightly oblique. Intervascular pit-pairs (Fig. 5) bordered, alternate to subopposite on the vessel wall, orbicular or angular where crowded, 8–10μ in diameter with circular or elongate aperture, occasionally confluent. Late-wood vessels small (Figs. 1, 4), 30–70μ in tangential diameter (mean 51μ), grouped in more or less continuous wing-like or festoon-like tangential or oblique bands, usually polygonal due to clustering, occasionally round to oval in form. Vessel elements 112–163μ in length, with spiral thickenings (Fig. 6). Perforation plates and intervascular pit-pairs similar to early wood vessels except slightly smaller. Thin-walled tyloses quite common.

Parenchyma: Paratracheal and metatracheal-diffuse. Paratracheal parenchyma (Fig. 4) quite abundant, contiguous to (but never forming a continuous sheath around) the large vessels of the early wood, marginal to and included in the clusters of smaller early-wood vessels and vascular tracheids (Fig. 4), and marginal to and included in the clusters of wavy bands of late-wood vessels and vascular tracheids. Diffuse parenchyma

sparse, scattered among the fibers, often in contact with the rays. Chambered parenchyma quite abundant (FIG. 7) usually consisting of eight or more elements per strand bearing crystals in a vertical series. Crystalliferous parenchyma usually associated with the xylem rays. (FIG. 3, 7).

Xylem rays: Homogeneous (Kribs Homogeneous Type 1) composed of procumbent cells (FIGS. 3, 7), 1–4 cells wide; uniseriate rays rather scanty, 2–10(14) cells high; multiseriate rays fusiform, mostly 3 or 4 cells broad and 0.76 mm. high; up to 6–10 rays per mm. Ray cells (FIG. 7) slightly thick-walled, circular to oval in tangential section and 10–15μ in diameter.

Imperforate tracheary elements: Libriform fibers and vascular tracheids. Libriform fibers circular to polygonal with rounded corners (FIG. 4) in cross-section, 10–15μ in diameter, the walls fairly thick, with a small lumen, nonseptate; interfiber pits simple. Vascular tracheids present both in the early-wood porous zone and in the wavy bands of late-wood vessels.

MATERIAL. A single specimen of silicified mature secondary xylem measuring 6 × 4 × 4 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55213.

Structural features of the fossil wood indicate, after extensive comparison, that its closest affinities are with the modern genus *Ulmus*. There is close agreement in all structural details except as noted below. A survey of all available woods of the genus *Ulmus* indicates that the nearest affinity of the fossil is with *U. americana* L. Our survey included the study of thin sections of the woods of 14 species of the genus supplemented by published descriptions of five other species. The latter are *U. sieboldii* Daveau (Kanehira, 1921a, p. 55, *pl. 6, figs. 34, 35*), *U. uyematsui* Hay. and *U. parvifolia* Jacq. (?) (Kanehira, 1921b, p. 211, *pl. 40, fig. 237*), *U. Wallichiana* Planch., and *U. lancifolia* Roxb. (Pearson and Brown, 1932, pp. 897–902, *figs. 279, 280*).

The size and distribution pattern of the vessels in the early wood of *Ulmus miocenica* and *U. americana* are almost identical, there being one or two rows of large vessels. However, the pattern of vessel arrangement in the late wood differs slightly in the fossil species. In *U. americana* there are usually almost parallel patches of small vessels separated from each other, whereas these patches are larger, closer, and slightly oblique in the fossil wood. Both in *U. americana* and in the fossil species the perforations are simple and the intervascular pit-pairs are bordered, usually alternate, orbicular or angular through crowding, and with circular to extended apertures.

The distribution of parenchyma appears to be almost identical in both, as is the fiber structure. However, a conspicuous difference between the two species is in the quantity of crystalliferous parenchyma which is quite frequent in the fossil wood but much less so in *Ulmus americana*.

The xylem rays of the fossil wood and of *Ulmus americana* are basically similar although there are slight differences in the height and breadth of the rays. In both they are closely spaced and homogeneous, composed of

procumbent cells of similar size and shape. However, the rays are 1–4 cells broad and up to 40 cells high in *U. miocenica*, whereas in *U. americana* they are up to 7 (mostly 4–6) cells broad and lower (up to 28 cells high: Brown, Panshin & Forsaith, 1949).

Determination of the degree of affinity to modern species of the genus leads to only a few observable differences between the Upper Miocene wood and that of the modern *Ulmus americana*. These differences are mainly limited to the distribution pattern of the late-wood vessels and the height and breadth of the xylem rays.

Sixteen species of fossil woods assigned to the family Ulmaceae have been reported hitherto. These have been described under the names *Ulminium* Unger (1842), *Ulmoxylon* Kaiser (1879), *Ulmus* L., *Zelkova* Spach, *Celtis* L., and *Celtoxylon*. Of these sixteen, five are recorded as species of extant genera, two each of *Zelkova* and *Ulmus*, viz., *Z. wakimizui* (Watari) Watari (1952), *Z. zelkoviformis* (Watari) Watari (1952), *Ulmus* sp. (Fietz, 1926a,b), *U. crystallophora* Watari (1952), and one of *Celtis* (Shimakura, 1936). The remaining eleven are designated as species of *Ulminium*, *Ulmoxylon*, and *Celtoxylon* (Pampaloni, 1904; Penhallow, 1907; Platen, 1908; Nagelhard, 1922; Greguss, 1943; Hofmann, 1944; Boureau, 1957).

Our fossil wood under consideration differs from all the species of *Ulminium* and *Ulmoxylon* and from both the fossil species of *Ulmus* recorded. Thus *Ulmus crystallophora* Watari, from the Miocene of Honsyu [Honshu], Japan, differs from *U. miocenica* in having 2–4-seriate large vessels in the early wood and in possessing rays 1–6 cells wide and up to 1020μ in height. However, in *U. miocenica* the large early-wood vessels are mostly in one row and the xylem rays are only 1–4 cells wide and up to 620μ in height.

It is interesting to note that a fossil wood, *Ulmoxylon simrothii*, showing resemblance to modern elms is also known from the Pliocene of California (Platen, 1908, pp. 26, 27, *pl. 1, figs. 5, 6*). This fossil wood differs from *Ulmus miocenica* in a number of features, especially in having small, radially elongated vessels (97.5μ in tangential diameter) mostly isolated in the early wood and forming a ring-like zone and in having numerous xylem rays five or six cells broad which are often weakly heterogeneous.

Ulmus, with about twenty species of small to very large trees, is widely distributed throughout the North Temperate Zone, except in the western half of North America. Of the six species native to the United States, three are of commercial importance. *Ulmus rubra* Mühl. (*U. fulva* Michx.) is of scattered occurrence over the entire eastern half of the country and southeastern Canada. *Ulmus thomasii* Sarg. occurs in western Vermont to extreme southern Quebec, New York, Ohio, Indiana, Kentucky, Illinois, Iowa, Missouri, and parts of adjoining states, being at its best in the Ohio Valley. *Ulmus alata* Michx. grows in the south-central states. *Ulmus americana* L. has a natural range including the eastern half of the United States, extending from the Great Plains to the Atlantic and from Canada to the Gulf of Mexico (Munns, 1938, *map 120*; Record and Hess, 1943).

Ulmus serotina Sarg. is known to inhabit banks and bluffs from southern Illinois and southern Kentucky to Arkansas, Georgia, and Alabama, and is thus one of the most restricted in geographic distribution. *Ulmus crassifolia* Nutt. prefers moist soil and is most abundant in river valleys from southwestern Tennessee, Arkansas to Mississippi, Louisiana, southern Oklahoma, Texas, and northern Mexico (Britton, 1908). The only species in tropical America is mexican elm, *U. mexicana* (Liebm.) Planch. growing in lower mountain regions from Veracruz and Oaxaca, Mexico, southward to Panama and northwestern Colombia (Record, 1924).

12. **Ulmus pacifica** Prakash & Barghoorn, sp. nov. (FIGS. 35–38)

Growth rings: Distinct (FIG. 37); wood semi-ring porous. Transition between early and late wood not very marked.

Vessels: Large vessels (FIG. 37) in the early wood, 70–160μ in tangential diameter (mean 114μ), chiefly solitary, arranged in one row, very rarely associated with small vessels, thin-walled, the solitary vessels usually circular to oval in cross-section. Perforation plates exclusively simple, horizontal to slightly oblique. Intervascular pit-pairs bordered, alternate to subopposite on the vessel wall (FIG. 36) oval to orbicular, 5–8μ in diameter and often somewhat loosely arranged, the aperture circular. Late-wood vessels (FIG. 37) slightly smaller, 40–120μ in tangential diameter (mean 76.5μ), almost always clustered in irregular groups, often forming radial rows, very rarely in wing- or festoon-like oblique bands, usually round to oval, sometimes variously shaped due to clustering. Vessel elements with spiral thickenings. Perforation plates and intervascular pit-pairs similar to early-wood vessels. Thin-walled tyloses quite common.

Parenchyma: Paratracheal and metatracheal-diffuse. Paratracheal parenchyma not abundant, occurring in association with the large early-wood vessels but never forming a continuous sheath, marginal to and sometimes included in the groups of late-wood vessels and vascular tracheids. Diffuse parenchyma very scanty, occurring as scattered cells among the fibers.

Xylem rays: Homogeneous (Kribs Homogeneous Type 2), composed of procumbent cells (FIG. 38), 1–8 cells wide, uniseriate and biseriate rays rare; uniseriate rays 2–9 cells high; multiseriate rays fusiform (FIG. 38), mostly 5–7 cells broad and 1.07 mm. high; up to 6–10 rays per mm. Ray cells thin-walled, circular to oval, sometimes vertically elongate in tangential section and 7–12μ in diameter.

Imperforate tracheary elements: Libriform fibers and vascular tracheids. Libriform fibers round to polygonal in cross-section (FIG. 35), 10–15μ in diameter, thick-walled, with a small lumen, non-septate; pits simple. Vascular tracheids often associated with the groups of late-wood vessels.

MATERIAL. A single specimen of silicified mature secondary xylem measuring 11 $\times$ 8 $\times$ 4 cm. Structural preservation of the fossil is poor.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55229.

There is close agreement with *Ulmus* in all structural details except as noted below. The fossil wood shows a superficial resemblance to the mature secondary xylem of *Ptelea*. However, the xylem rays of *Ptelea* are heterogeneous and the vessels are devoid of tyloses, whereas the fossil possesses homogeneous rays and the vessels are tylosed.

The fossil wood does not compare in all details with any extant species of *Ulmus*, but it shows some structural resemblance with *Ulmus mexicana* (Liebm.) Planch. Although both in the fossil and *Ulmus mexicana* the vessel distribution is semi-ring-porous and there is little difference in vessel size in the early- and late-wood zones, the frequency of the vessels in the fossil wood is greater than in *U. mexicana* in which the vessel groups or rows are smaller and more widely separated than the fossil under consideration. However, the vessel perforations and intervascular pit-pairs are similar in both.

The distribution and amount of parenchyma is different in the fossil and extant *Ulmus mexicana*. The paratracheal parenchyma is more abundant in *U. mexicana* than in *U. pacifica* and the metatracheal parenchyma often forms broken tangential bands one to three cells wide in *U. mexicana*. Such parenchyma bands are not known in the fossil under consideration. Furthermore, in *U. mexicana* there are usually several layers of parenchyma cells associated with the growth rings, a type of parenchyma not found in *U. pacifica*; and crystalliferous parenchyma is quite common in *U. mexicana* but lacking in the fossil wood.

The xylem rays of the fossil wood and of *Ulmus mexicana* are basically similar, although there are some differences in height and breadth. In both they are closely spaced and homogeneous, composed of procumbent cells. However, the rays are 1–8 cells broad and 1.07 mm. high in *U. pacifica*, whereas in *U. mexicana* they are only 1–6 cells broad and lower, including uniseriate and biseriate rays quite frequently. Uniseriate and biseriate rays are very rare in the present fossil wood.

Lastly, the fiber structure appears to be almost identical in both. The fibers are nonseptate, thick walled, and usually polygonal in cross-section, with simple pits.

The general agreement in, as well as the numerous microscopic details of, anatomical structure provides sufficient evidence to identify the Vantage fossil wood as *Ulmus*. However, there are no extant species of *Ulmus* with which the fossil wood can be compared very closely. Therefore, it is quite possible that the fossil wood belongs to an extinct species somewhat differing from modern *Ulmus* species but exhibiting the general anatomical organization of the genus.

DISCUSSION

The present study of the petrified woods from the Columbia Basalts at Vantage has given valuable information regarding the changes in the forest vegetation of the western United States since Miocene times. In the present paper, the authors describe fossil woods of *Acer*, *Diospyros*,

Quercus, *Liquidambar*, *Carya*, *Albizzia*, *Gleditsia*, *Platanus*, and *Ulmus*. A study of the present-day distribution of these genera reveals important clues to the migration of these forms since the Upper Miocene. At present, the genera *Diospyros*, *Liquidambar*, *Carya*, *Gleditsia*, and *Ulmus* are largely limited to the eastern United States. On the other hand, the genus *Platanus* grows in both the eastern and the southwestern United States, while *Acer* and *Quercus* occur almost throughout. The genus *Acer* attains its greatest development in eastern Asia and the eastern United States and only a few species are now found in the western part of the country. Among the species of *Quercus*, *Q. alba* L., with which the fossil wood of *Q. leuca* Prakash & Barghoorn compares well, grows throughout the entire eastern half of the United States. *Albizzia*, at present, is widely distributed in tropical Asia, Africa, and America. However, *A. julibrissin* Boiv., an Asiatic tree, long planted for ornament and shade in the southern United States, has become naturalized from Virginia to Florida and Louisiana. From this, it is evident that the Vantage forest is composed of the eastern, the western, and the exotic elements, particularly those of Asia. It, therefore, seems quite likely that during the Miocene the present forest vegetation of this country was more widely distributed than at the present time. It appears to have become restricted after the Miocene as a result of climatic and orographic change. The complete extinction of the deciduous forest at Vantage and neighboring areas seems to have been accelerated with the late Tertiary rise of the Cascade Mountains and their concomitant effect on depleting the moisture from the Pacific air masses. The effect of increasing cold resulting from the oncoming Pleistocene and the failure of remigration in post-glacial times also helped to accelerate this process. A further study of this flora, which will throw more light on the past vegetation of the northwest United States, its trend of migration, and a number of other related problems, is in progress.

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EXPLANATION OF PLATES

PLATE 1

FIGS. 1–7. Wood of *Ulmus miocenica*: 1, transverse section, × 26 — note the ulmiform bands of late-wood vessels; 2, tangential section, × 75; 3, tangential section showing shape, size, and distribution of xylem rays, × 26 — also note chambered parenchyma associated with rays; 4, transverse sections showing the cellular structure of various tissues, × 100; 5, intervascular pitting, × 320; 6, spiral thickening of late-wood vessels, × 130; 7, tangential section showing a xylem ray and chambered parenchyma, × 100. FIGS. 8–9. Wood of *Platanus americana*: 8, intervascular pitting, × 320; 9, transverse section showing the details of the structure, × 75.

PLATE 2

FIGS. 10–13. Wood of *Platanus americana*: 10, transverse section, × 26 — note vessel distribution and growth rings forming a notch where they meet the rays; 11, tangential section showing shape and size of xylem rays, × 26; 12, scalariform perforation plate, × 90; 13, simple perforation plate, × 90. FIGS. 14–18. Wood of *Carya tertiara*: 14, swollen chambered parenchyma with crystals, × 110; 15, transverse section, × 40 — note the distribution of metatracheal parenchyma cells often with crystals; 16, tangential section showing form and distribution of the rays, × 35; 17, tyloses in the vessels, × 90; 18, intervascular pitting, × 90.

PLATE 3

FIG. 19. Wood of *Carya tertiara*: 19, transverse section, × 26 — note the vessel and parenchyma distribution. FIGS. 20–24. Fossil wood of *Liquidambar styraciflua*: 20, transverse section, × 26 — note vessel distribution; 21, tangential section, × 90; 22, scalariform perforation plate, × 150; 23, intervascular pitting, × 230; 24, transverse section, × 150. FIGS. 25–27. Wood of *Acer puratanum*: 25, transverse section, × 90; 26, spiral thickenings, × 90; 27, transverse section, × 26 — note vessel distribution.

PLATE 4

FIG. 28. Wood of *Acer puratanum*: 28, tangential section showing shape and size of the xylem rays, × 90. FIG. 29. Wood of *Gleditsia columbiana*: 29, transverse section, × 65 — note vessel distribution in the late wood. FIG. 30. Wood of *Acer puratanum*: 30, intervascular pitting, × 190. FIGS. 31–34. Wood of *Gleditsia columbiana*: 31, intervascular pitting, × 280; 32, spiral thickening, × 310; 33, tangential section, × 65 — note ray distribution; 34, transverse section, × 26 — note vessel distribution in early and late wood. FIGS. 35–36. Wood of *Ulmus pacifica*: 35, transverse section, × 125; 36, intervascular pitting, × 220.

PLATE 5

FIGS. 37, 38. Wood of *Ulmus pacifica*: 37, transverse section, × 40 — note vessel distribution; 38, tangential section, × 50 — note xylem rays, tyloses in vessels. FIGS. 39–43. Wood of *Quercus leuca*: 39, transverse section showing parenchyma and fiber cells, × 140 — note slightly enlarged cells of parenchyma often with crystals; 40, tracheid pitting, × 310; 41, transverse section showing late-wood vessels, × 65 — note thin-walled, angular pores; 42, transverse section showing the distribution of metatracheal parenchyma, × 65; 43, transverse section, × 26 — note large vessels in early wood and smaller vessels in late wood arranged in flame-shaped tracts.

PLATE 6

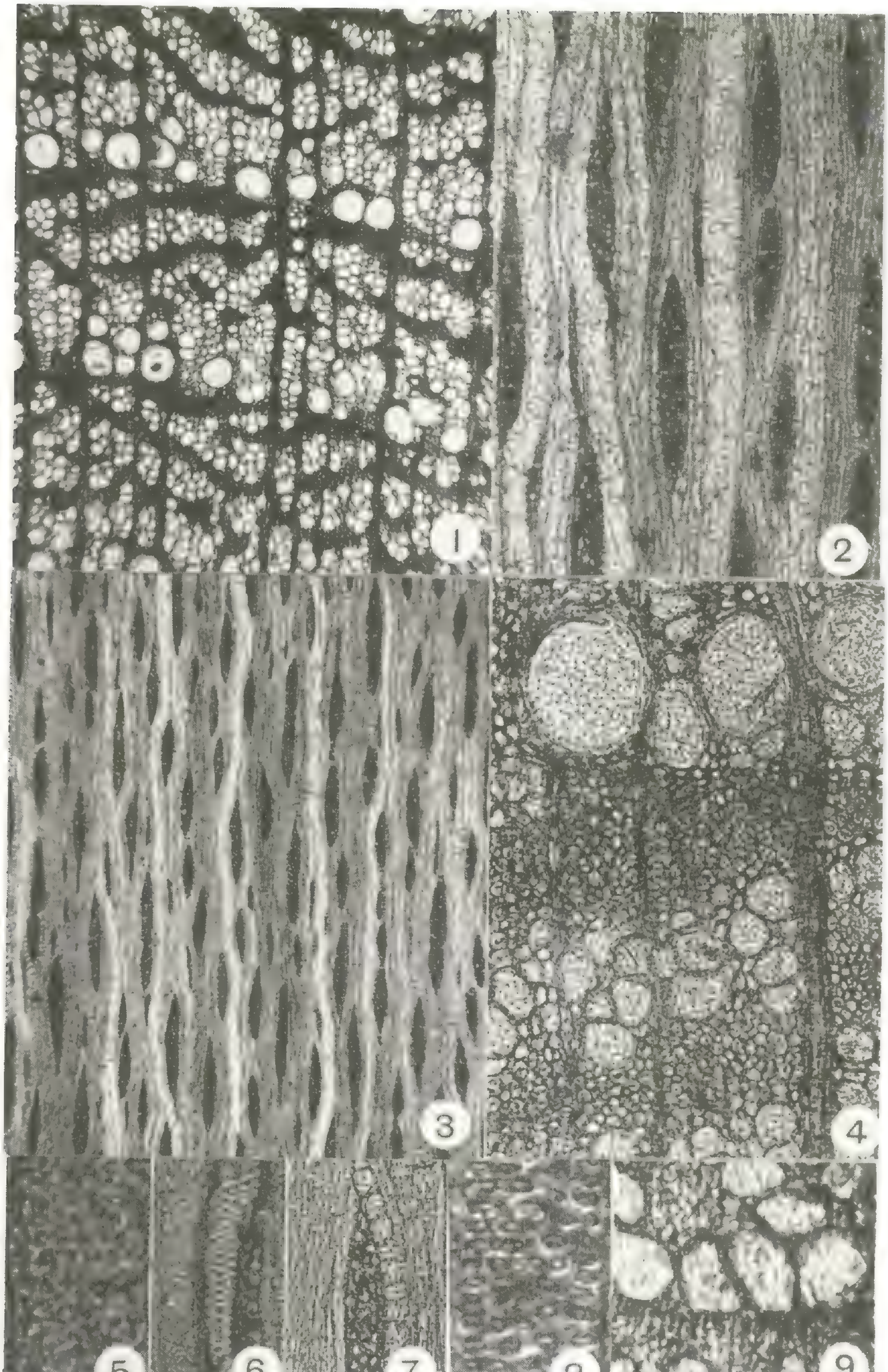
FIGS. 44, 45. Wood of *Quercus leuca*: 44, tangential section, × 75 — note part of an aggregate ray and numerous uniseriate rays; 45, another transverse section showing three growth-zones, × 18 — note the distribution of vessels in early and late wood. FIGS. 46–50. Wood of *Diospyros washingtoniana*: 46, part of tangential section showing the ray structure, × 105; 47, transverse section showing vessel distribution, × 35; 48, tangential section, × 40 — note the storied arrangement of the xylem rays; 49, part of transverse section highly magnified, × 70 — note thick vessel wall; 50, tyloses, × 90. FIG. 51. Wood of *Albizzia vantagiensis*: 51, intervascular pitting, × 280.

PLATE 7

FIGS. 52–54. Wood of *Albizzia vantagiensis*: 52, transverse section, × 26 — note vessel and parenchyma distribution forming eyelets around vessels; 53, tangential section, × 65 — note shape, size, and distribution of xylem rays; 54, transverse section magnified to show parenchyma distribution, × 65. FIGS. 55–57. Wood of *Acer beckianum*: 55, transverse section, × 50 — note vessel distribution and broad xylem rays; 56, part of Fig. 55 magnified to show structural details, × 80; 57, intervascular pitting, × 220.

PLATE 8

FIG. 58. Wood of *Acer beckianum*: 58, tangential section, × 65. FIGS. 59–63. Wood of *Acer olearyi*: 59, simple perforation and spiral thickening, × 225; 60, intervascular pitting, × 225; 61, transverse section, × 105; 62, transverse section, × 38 — note solitary vessels and narrow rays; 63, tangential section showing xylem rays, × 105.



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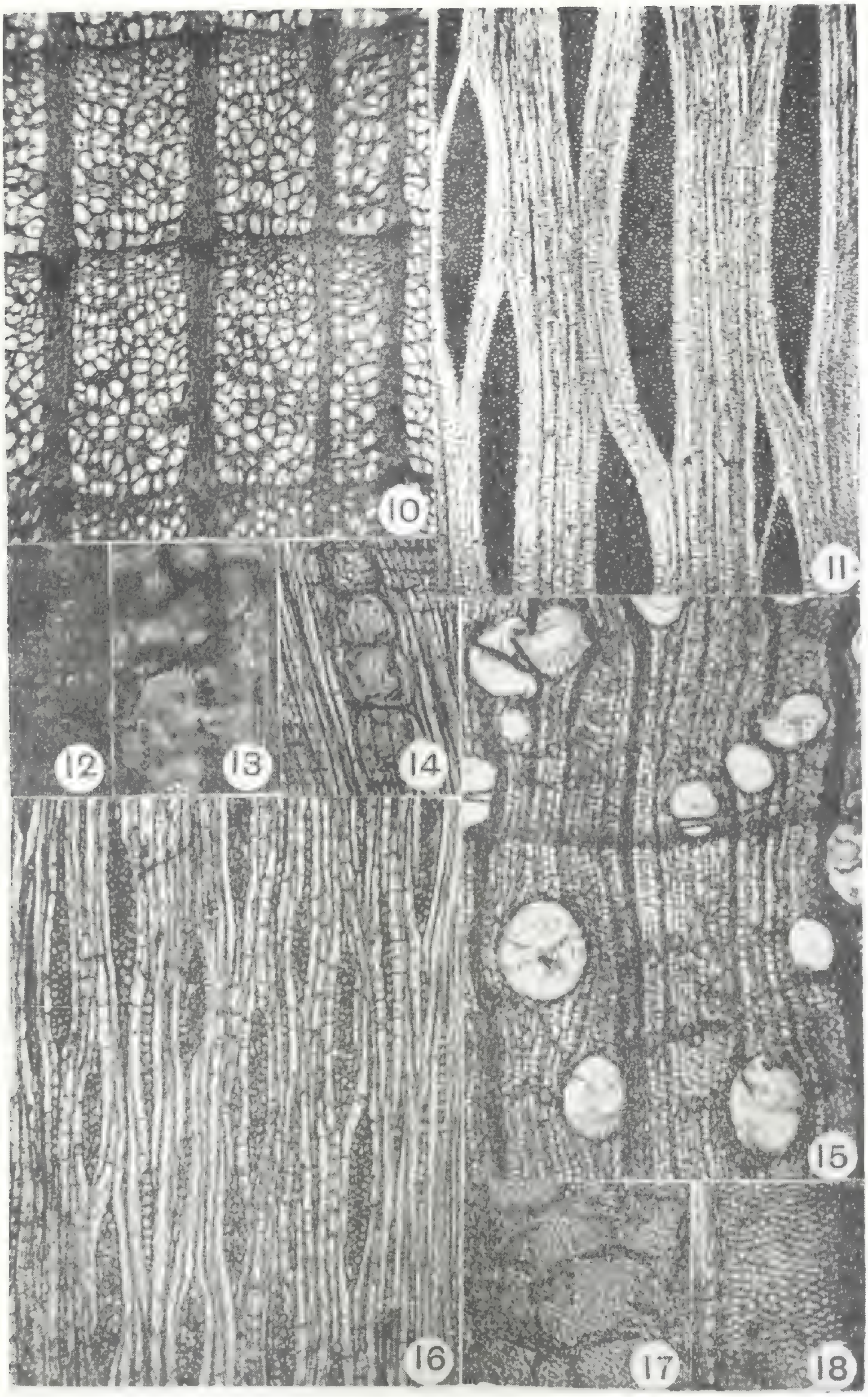
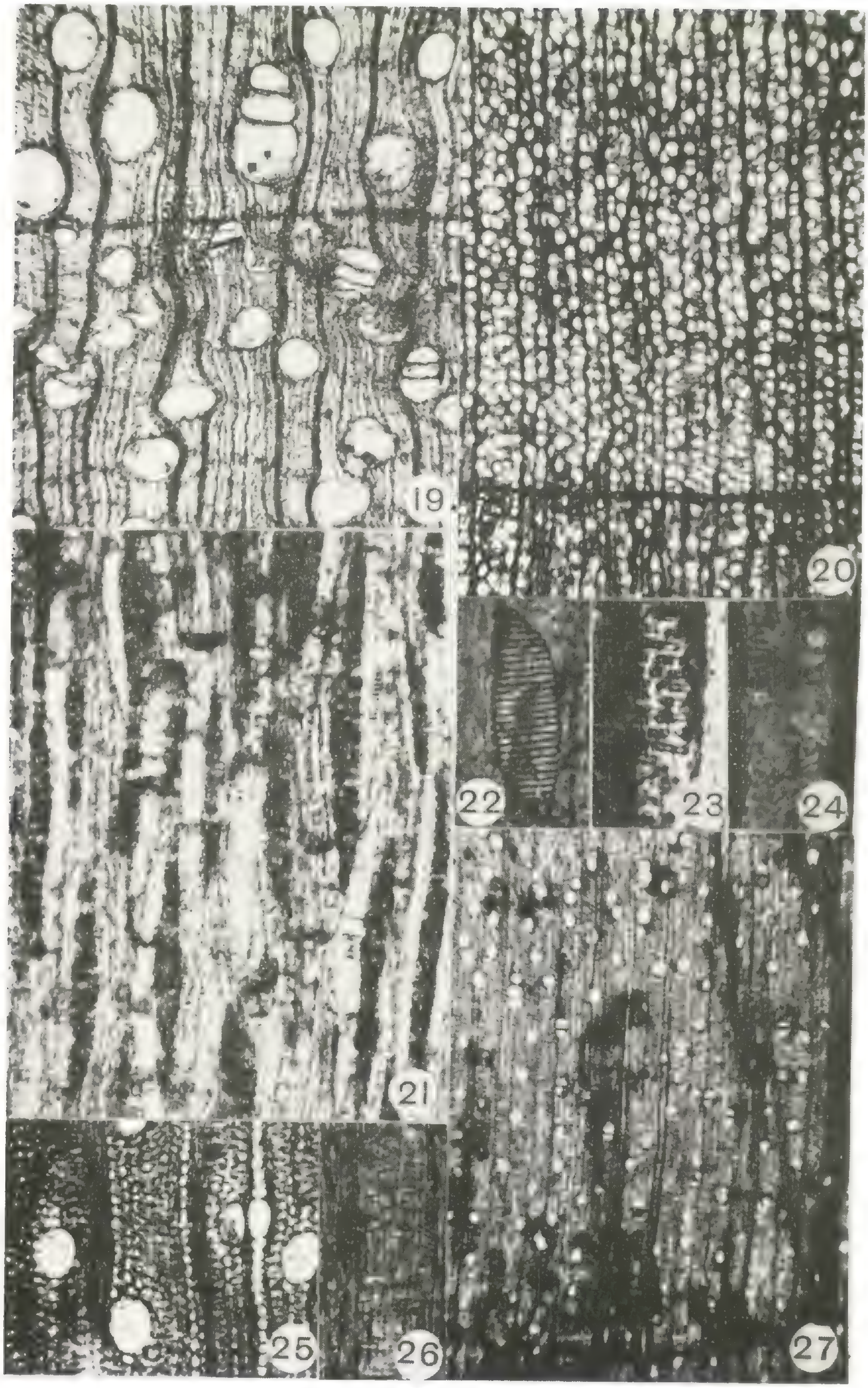


PRAKASH & BARGHOORN, MIOCENE WOODS



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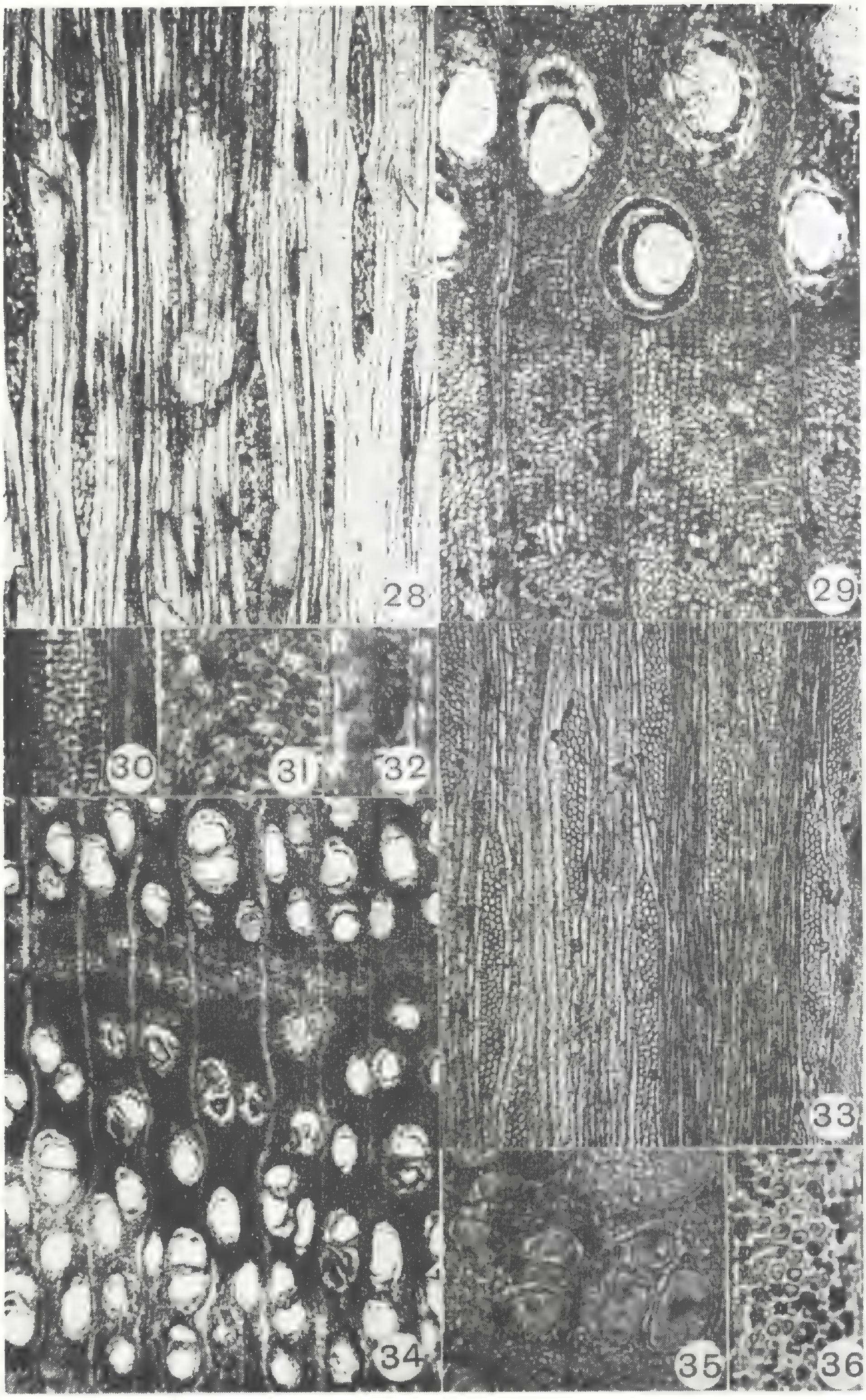

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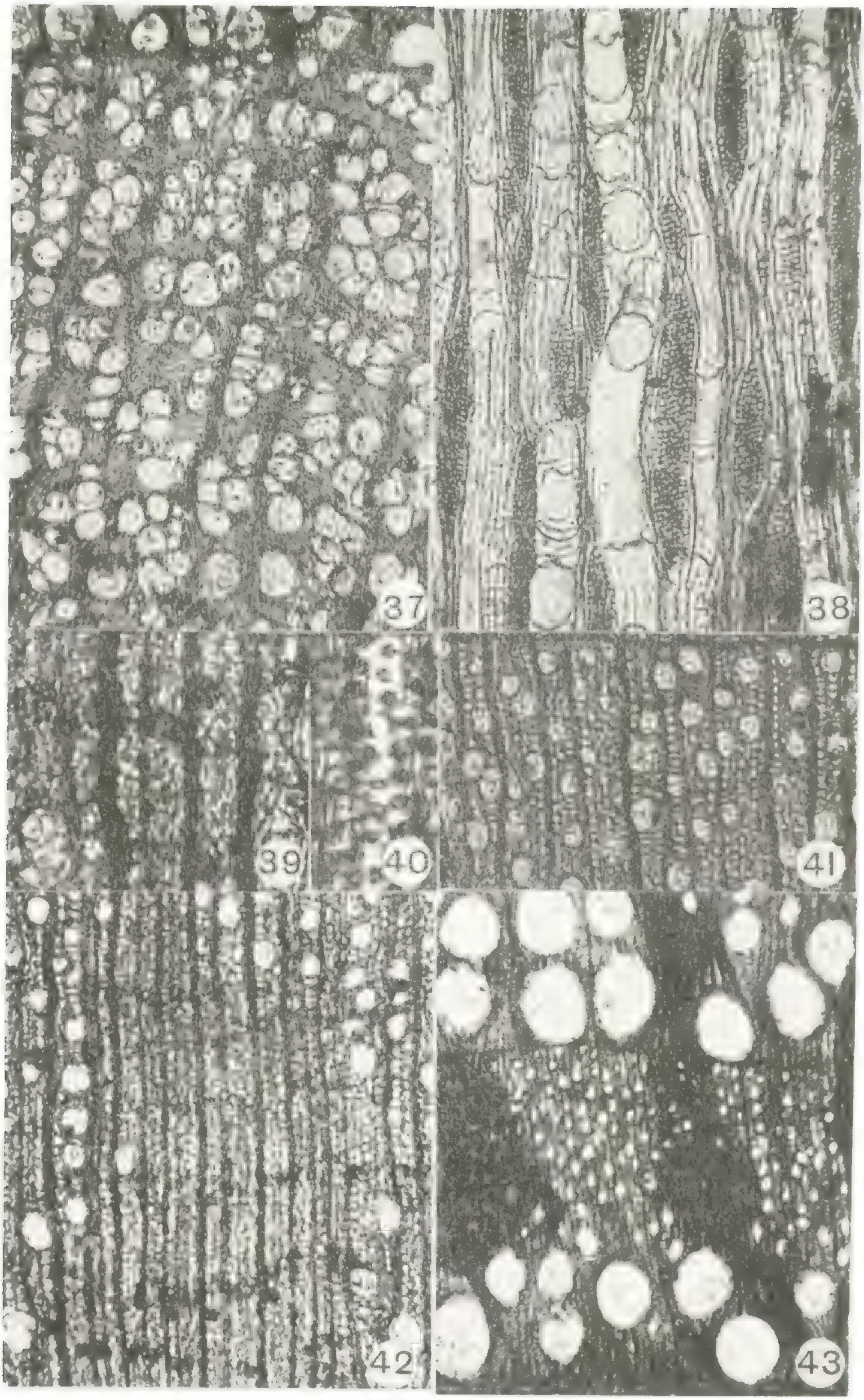

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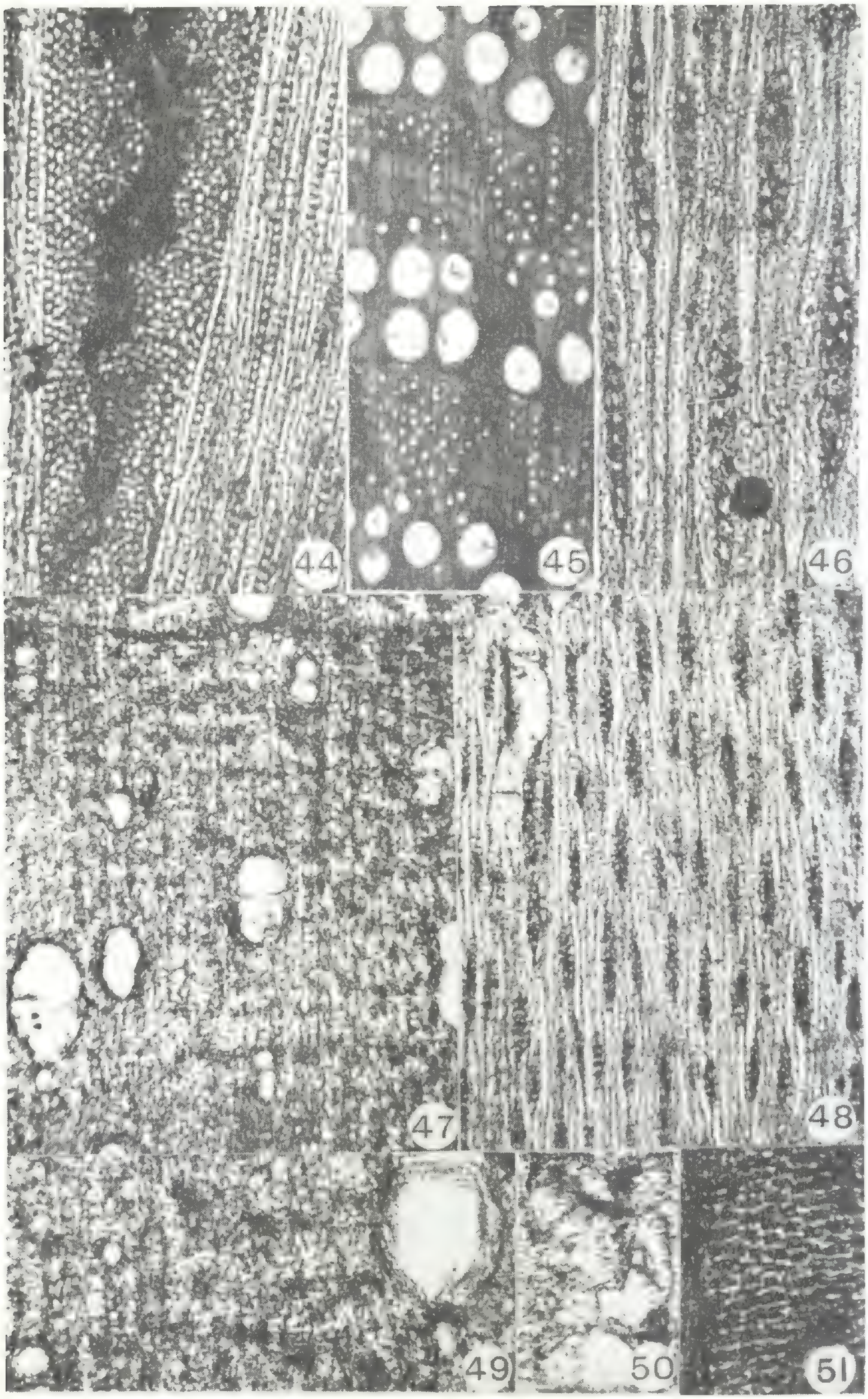

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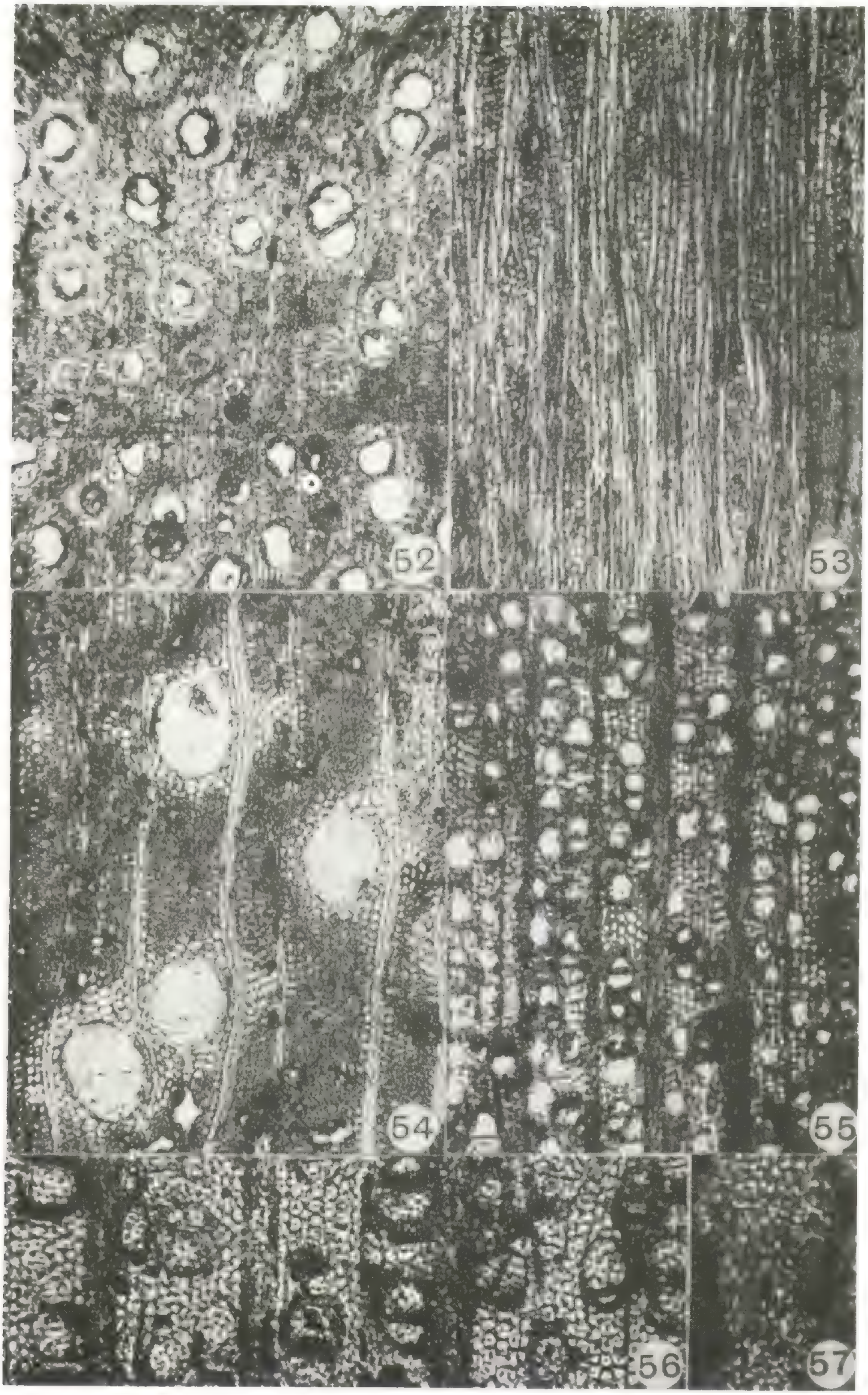

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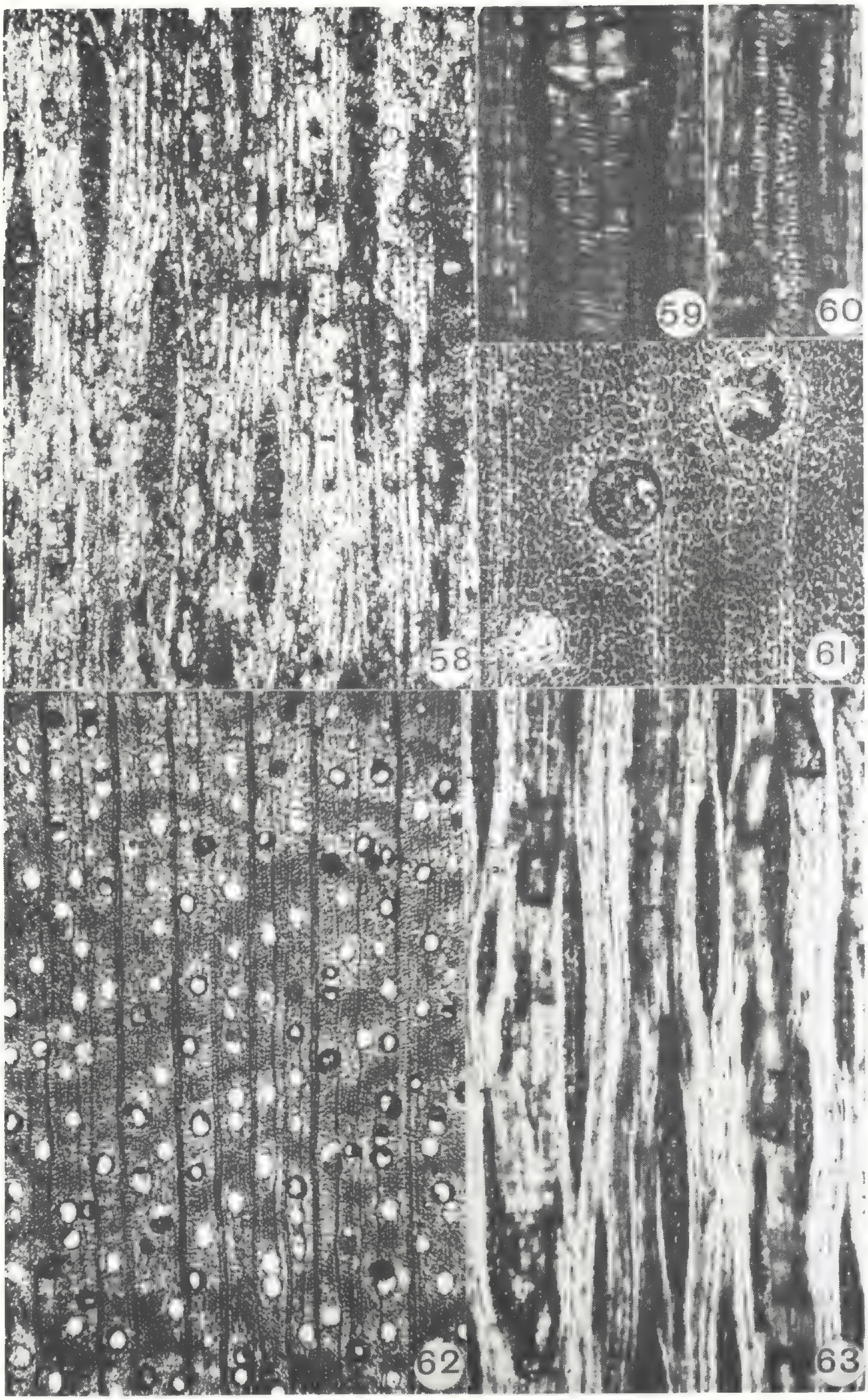

PRAKASH & BARGHOORN, MIOCENE WOODS

THE GENERA OF TURNERACEAE AND PASSIFLORACEAE IN THE SOUTHEASTERN UNITED STATES *

GEORGE K. BRIZICKY

TURNERACEAE A. P. de Candolle, Prodr. 3: 345. 1828.
(TURNERA FAMILY)

Herbs or shrubs [rarely trees], usually pubescent. Leaves alternate, simple, toothed to entire [rarely pinnately divided], stipules small or absent. Flowers regular, bisexual, 5-merous, often heterostylous, axillary, solitary [or in terminal and/or axillary heads, racemes, cymes, or rarely panicles], typically 2-bracteolate. Floral tube (hypanthium) sometimes very short, deciduous after anthesis, often bearing 5 protuberances or glands just above the insertion of stamens and rarely a narrow, fringed corona within the petals. Sepals imbricate, on the rim of the floral tube. Petals distinct, perigynous, contorted in aestivation. Stamens 5, alternipetalous, usually inserted in the floral tube; filaments free; anthers introrse, dorsifixed near base, 2-locular at anthesis, dehiscing longitudinally; pollen grains ellipsoidal (prolate), mostly large, usually 3-colpate, reticulate. Gynoecium syncarpous, 3-carpellate; stigmas usually brushlike; styles 3, terminal, filiform, simple or dichotomously divided; ovary superior, sessile, 1-locular; placentae 3, parietal, each with 1 to numerous anatropous ovules with 2 integuments and thick nucellus [or placenta very rarely single, basal, uniovulate]. Capsule 1-locular, 3-valved, usually loculicidal and 3- to many-seeded [rarely septicidal and 1-seeded]; seeds with a membranaceous, unilateral aril; seed coat alveolate-striate; endosperm fleshy; embryo large, axile, straight or slightly curved. Type genus: *Turnera* L.

A family of eight genera with about 120 species distributed primarily in tropical America (two genera, one exclusively, the other predominantly American, with about 100 species), in tropical Africa (six genera with about 17 species), Madagascar (two genera, one monotypic), and Rodriguez Island in the Mascarene group (one monotypic, endemic genus).

* Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Gray Herbarium and the Arnold Arboretum made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Reed C. Rollins and Carroll E. Wood, Jr. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39**: 296–346. 1958). Other published portions of these studies will be found in Jour. Arnold Arb. **40–42.** 1959–1961. The area covered in this, as in former treatments, is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. Data included in descriptions which are inapplicable to our species are placed in brackets. References which have not been checked are marked by an asterisk. The illustration has been made by Dorothy H. Marsh under the direction of C. E. Wood, Jr. Messrs. R. A. Howard, R. B. Channell, and H. F. L. Rock have kindly provided some of the fresh material used for illustration and/or study.

Diverse kinds of hairs (glandular and both simple and stellate non-glandular trichomes) which usually occur on the stems, leaves, pedicels, calyces, and fruits are of considerable taxonomic importance. Extrafloral nectaries are sometimes present at the base of the leaf blade ("basal glands") or on the petiole. The occasional occurrence of scalariform perforation plates in the secondary xylem (*Turnera Hindsiana* Benth.) or at least in the neighborhood of the primary xylem (*Turnera* spp., *Piriqueta* spp.) is noteworthy. Tanniniferous cells in leaves (epidermis) and primary cortex are of common occurrence.

The flowers of Turneraceae are recorded as ephemeral. According to Rao the floral tube ("calyx tube" or "hypanthium") is appendicular in nature, and the perigyny (in *Turnera*) has resulted from the adnation of the basal parts of sepals, petals, and stamens. A corona occurs only in *Piriqueta*. Almost 70 per cent of the species of the family have been recorded (by Urban) as having heterostylous flowers, the remaining having homostylous or (rarely) incompletely heterostylous flowers. In Turneraceae homo- and heterostyly seem to be characters of specific significance. Cross-pollination seems to be the rule, but, in homostylous and incompletely heterostylous flowers self-pollination (with self-fertilization) has been recorded in the case of failure of insect visitors, the withering corolla then bringing the anthers into contact with the stigmas. Bees have been reported as pollination agents in a few cases. The embryology of Turneraceae, studied in *Turnera ulmifolia*, essentially agrees with that of *Passiflora*. The germination power of seeds has been recorded (Urban) as lasting only a few years and as being low even in fresh seeds. No chromosome counts are known.

A close relationship of Turneraceae with Passifloraceae and Malesherbiaceae has been generally assumed by taxonomists. This view is supported by evidence from anatomy, palynology, and embryology (the last in regard to Passifloraceae). Malesherbiaceae seem to be a link between Turneraceae and Passifloraceae.

The family is of no economic importance.

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KEY TO THE GENERA OF TURNERACEAE

Peduncle distinct, flower pedicellate, ebracteolate; floral tube with a fimbriate corona in the throat just within the petals; styles more or less deeply divided; leaves without basal glands, stellate hairy or glabrous. 1. *Piriqueta*.

Peduncle adnate to the petiole, flower sessile or subsessile, 2-bracteolate at base; corona absent; styles simple; leaves 2-glandular at base of blade, hairs simple. . . . . 2. *Turnera*.

1. **Piriqueta** Aublet, Hist. Pl. Guiane Fr. 1: 298. 1775.

Erect herbs [rarely shrubs or trees], usually stellate-pubescent and often hirsute, rarely glabrous. Leaves alternate, petiolate or sessile, crenate or serrate (teeth often glandular or glanduliferous), rarely entire, exstipulate [rarely stipulate]. Inflorescences basically axillary and cymose (monochasial), often reduced to solitary flowers with a distinct peduncle jointed with the pedicel in the axils of upper leaves or bracts and forming bracted [or bractless] "racemes"; bracteoles absent or minute. Flowers heterostylous [or homostylous]. Floral tube turbinate or turbinate-campanulate, 10-ribbed, often with 5 fleshy liguliform or semiorbicular, cushion-like protuberances (extrastaminal nectaries) just above the insertion of the stamens. Sepals 5, on the margin of the floral tube. Petals 5, perigynous, cuneate or slightly unguiculate, yellow [or pink, purple, blue, or white]. Corona membranaceous, fringed, often inconspicuous. Stamens 5, filaments gradually broadened toward the base, inserted in the floral tube near its base; anthers ovate to oblong, usually obtuse or truncate at apex,

emarginate at base, the top often recurved after anthesis. Stigmas brush-like; styles 3, filiform, each more or less deeply dichotomously (rarely trichotomously) divided; ovary 1-locular, with numerous ovules on 3 parietal placentae. Capsule globose or ellipsoidal, smooth [or tuberculate], appressed-pubescent with simple hairs or glabrous, septicidal, 3-valved almost to the base; seeds numerous, straight or slightly curved, alveolate-striate; aril unilateral, crenate [to lacerate], as long as or shorter than the seed. TYPE SPECIES: *P. villosa* Aubl. (*P. cistoides* (L.) Griseb. var. *latifolia* Urb.). (Name derived from *piriquete*, the name of this plant in French Guiana.)

A genus of about 30 species, primarily of the American tropics, with its center of distribution in Brazil, but one species extending into the warmer temperate zone of eastern North America; in the Old World, three species in Madagascar and one in South Africa.

Only the South American–West Indian *P. caroliniana* (Walt.) Urb., a perennial herb with yellow, heterodistylous flowers, occurs in our area from the Florida Keys northward on the Coastal Plain to southwestern Georgia and eastern North Carolina. The species varies considerably in shape of leaves (obovate- or elliptic-oblong or lanceolate to narrowly linear) and pubescence of stems and leaves (stellate-tomentose and hirsute to stellate-hairy to glabrous). On this basis, five different varieties, four treated by Small (Man. Southeast. Fl.) as separate species, have been recognized in our area: var. *caroliniana*; var. *tomentosa* Urb. (*P. tomentosa* sensu Small, not HBK.); var. *glabra* (DC.) Urb. (*P. glabrescens* Small); var. *viridis* (Small) G. S. Torrey (*P. viridis* Small); and var. *exasperata* Urb. (*P. Tracyi* Gand.), the last differing from var. *glabra* only in the stellate pubescence of the leaves and perhaps included by Small in his *P. tomentosa*. Urban regarded *P. tomentosa* HBK., which does not occur in our area, as conspecific with *P. villosa* Aubl. and treated it as *P. cistoides* var. *latifolia*. The entire genus is much in need of a modern taxonomic revision, and field observations, culture experiments, and cytogenetic studies are needed to determine the status (probably intraspecific) of the variants in our area. Our species is closely related to and very often confused with *P. cistoides*, which has approximately the same range in the West Indies and South America as *P. caroliniana*, but which differs mainly in the homostylous and somewhat smaller flowers.

Agents of seed dispersal are unknown, but myrmecochory appears probable.

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2. **Turnera** Linnaeus, Sp. Pl. 1: 271. 1753; Gen. Pl. ed. 5. 131. 1754.

Perennial [or annual] herbs, often woody at base, or shrubs [rarely trees], usually pubescent with simple [rarely stellate] hairs [or glabrous]. Leaves petiolate [or sessile], coarsely serrate [or crenate, rarely somewhat pinnately divided or entire], often 2-glandular at the base of the blade [or at the apex of the petiole], stipules minute or wanting. Inflorescences uniflorous in the axils of the upper leaves [rarely cymose or capitate], peduncles united with the petioles of subtending leaves [rarely free]. Flowers homostylous [or heterostylous], subsessile [or sessile], conspicuously 2-bracteolate at base. Floral tube cylindrical, broadened at apex [or hemispherical, campanulate, or turbinate], usually shorter than the sepals, sometimes bearing 5 alternipetalous semiorbicular projections above the insertion of stamens. Petals obovate, short-clawed, perigynous, yellow [more rarely pink, crimson, purple, blue, or white]. Stamens 5, inserted near the base of the floral tube, the lower parts of the filaments broadened and adnate by their membranaceous margins to the wall of the tube forming 5 nectar pockets; anthers narrowly ovoid-conical, acute at apex, emarginate at base. Stigmas brushlike [or fanlike]; styles 3, simple; ovary 1-locular, with numerous ovules on 3 parietal placentae. Capsule globose [or ovoid], verrucose [smooth or impressed-reticulate], hairy [rarely glabrous], rather thick-walled, 3-valved to below the middle [or to the base], the valves often recurved at apex. Seeds cylindric-clavate [or obovoid], straight or somewhat curved, alveolate-striate, glabrous [or puberulous], hilum often conspicuous, semiglobose [or conical]; aril whitish, lobed [crenate or lacerate], as long as or shorter than the seed. TYPE SPECIES: *T. ulmifolia* L. (Named in honor of William Turner, 1515–1568, physician and herbalist, the "Father of English Botany.")

An entirely American genus of about 70 species occurring from Argentina to Texas. *Turnera ulmifolia*, a polymorphic species including about 12 varieties (six of which are heterostylous), is distributed throughout the range of the genus (except Texas). The West Indian var. *ulmifolia* (var. *angustifolia* Willd.) has been recorded as naturalized in our area on the Florida Keys and in peninsular Florida (and on the Coastal Plain from Florida to Louisiana, according to Small [Man. Southeast. Fl. 1933]). This variety and *T. subulata* J. E. Smith (*T. ulmifolia* var. *elegans* (Otto) Urb.) are now rather widely naturalized in the East Indies, Ceylon, Malaya, Indonesia, Seychelles, and Madagascar. Seed dispersal by ants has been recorded in both these species, and the other species of *Turnera* apparently are also myrmecochorous.

Dried leaves of *Turnera diffusa* Willd., of tropical America, Mexico, and Texas (here var. *aphrodisiaca* (Ward) Urb.), known as "damiana," have been used locally as a tonic and aphrodisiac. Infusions of leaves of *T.*

ulmifolia have been recorded as efficient against dysenteries on Java, while *T. opifera* Mart. has a similar reputation in Brazil; leaves of both are also utilized locally as tonics, expectorants, and/or astringents.

The genus is in need of a modern taxonomic revision.

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PASSIFLORACEAE Jussieu ex HBK. Nov. Gen. Sp. **2:** 126. 1817, 'Passifloreae,'

(PASSION-FLOWER FAMILY)

Herbaceous or woody plants climbing by axillary tendrils [rarely erect, without tendrils]. Leaves alternate, simple [or very rarely compound], stipulate, petioles often with extrafloral nectaries (glands). Inflorescences axillary, bracteate, cymose (di- or monochasial), usually associated with a terminal or collateral tendril, sometimes reduced to geminate or solitary 1-flowered peduncles. Flowers regular, bisexual [rarely unisexual], 5[4, rarely 3]-merous, complete, rarely apetalous. Sepals and petals imbricate, perigynous; the floral tube usually with a "corona." Stamens 5[–10], alternipetalous, hypogynous, free from the gynophore or raised on an androgynophore, anthers versatile, 2-locular at anthesis, longitudinally dehiscent. Gynoecium 3[–5]-carpellate; stigmas capitate, clavate, or discoid; styles 3 [or 1–5]; ovary stipitate, rarely sessile, 1-locular, with numerous anatropous ovules on 3[–5] parietal placentae. Fruit a berry [or capsule]; seeds arillate with straight embryo and fleshy endosperm. TYPE GENUS: *Passiflora* L.

A primarily tropical family composed of 12 genera with over 500 species discontinuously distributed over a considerable part of the tropical zone. Eight of the genera (five monotypic) are restricted to the Old World, three (*Dilkea*, *Mitostemma*, and *Tetrastylis*) are exclusively American, and one (*Passiflora*) is preponderantly New World.

The presence of a "corona" (in combination, however, with the usually climbing habit, the cymose inflorescences associated with tendrils, the stipitate ovary, and the arillate seeds) is perhaps the most outstanding feature of the family. Absent only in *Machadoa* and two (of six) sections

of *Adenia*, the "corona" occurs in all the other members of Passifloraceae. In its simplest form (*Adenia*, *Crossostemma*, *Tetrapathaea*) it consists of a membrane or a ring of threads, situated at the rim of the floral tube; in the most complex form (*Passiflora* and *Tetrastylis*) it is composed of many series of threads, membranes, folds, etc. This complexity requires a special descriptive terminology for the various parts of the "corona," which differ in appearance and/or size, position in the floral tube, and biological function. The terminology used by Killip (based on Harms) in his monograph of the family is followed here. The following subdivisions of the "corona" are generally recognized: the *corona* (sensu stricto), *operculum*, *nectar ring* or *annulus*, and *limen*. (See illustration.)

Passifloraceae are closely allied with Turneraceae, Malesherbiaceae, and Flacourtiaceae–Paropsieae. Some relationship with Cucurbitaceae through Achariaceae is also presumed by some taxonomists. A close affinity with Caricaceae appears somewhat questionable. In its present delimitation, based mainly on biological characters (e.g., climbing habit) and gross morphology of the flowers, the family appears to be fairly natural. There are, however, some evidences from the wood anatomy and palynology which suggest a taxonomic re-evaluation of Passifloraceae and their closest allies (especially Flacourtiaceae Paropsieae), based on data from comparative anatomy and other botanical disciplines. Our knowledge of the family as a whole in regard to the cytogenetics, embryology, and floral anatomy is rather limited, being almost exclusively based on studies on a relatively small number of species of *Passiflora*.

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1. **Passiflora** Linnaeus, Sp. Pl. 2: 955. 1753; Gen. Pl. ed. 5. 410. 1754.

Herbaceous or woody vines [rarely erect herbs, shrubs, or small trees]. Leaves alternate, simple [rarely compound), predominantly 3–5-nerved from the base, undivided or more frequently palmately [2]3–5-lobed, entire or toothed, petiolate, the petiole often glanduliferous, stipules setaceous to broadly ovate, sometimes foliaceous, entire, toothed or deeply cleft, usually persistent. Tendrils axillary, simple. Inflorescences axillary, usually reduced to solitary or paired 1-flowered (rarely 2–10-flowered) peduncles, sometimes flowers fascicled [or arranged in dichasial or raceme-like inflorescences]. Bracts (bract and bractlets) usually present, small and scattered or relatively large (sometimes foliaceous) and verticillate, forming an involucre near the base of the flower. Floral tube patelliform, cupuliform, funnelform, or campanulate [sometimes short- or long-tubular], rounded or impressed at base. Sepals 5, membranaceous or subcoriaceous, often more or less petaloid, sometimes dorsally appendaged (corniculate, etc.) just below the apex. Petals 5, membranaceous, delicate, greenish, white or highly colored, as long as or shorter than the sepals, usually situated at the margin of the floral tube just within the sepals [rarely attached below the mouth of the floral tube], sometimes absent. Corona of 1 to several series of distinct or more or less united processes, sometimes high colored and/or variegated in various shades [rarely membranaceous]; operculum borne within or below the corona, membranaceous, flat or plicate, entire, dentate or fringed, [sometimes filamentous, rarely absent]; nectar ring within or below the operculum, sometimes absent; limen borne at or above the base of the androgynophore or encircling the base of sessile ovaries, sometimes absent. Stamens 5, usually raised on an androgynophore, filaments free, attached to the back of the anthers near their middle; anthers linear to oblong, at first introrse, appressed to the sides of the ovary, extrorse when mature; pollen grains large, globose to ellipsoid, reticulate, 3–12-colpate. Gynoecium syncarpous, borne on an elongated gynophore, very rarely sessile or subsessile; styles usually 3, distinct or united at the base, cylindric or clavate, each with a capitate or reniform stigma; ovary 1-locular, usually with 3 parietal placentae, each with 2–4 rows of 2-integumented ovules with a thick nucellus. Fruit a small to very large, ovoid, ellipsoidal or globose berry; seeds several to many, covered by a fleshy aril open only at the apex, ± laterally compressed, oblong to suborbicular in outline, with an outer thin, mem-

branaceous sarcotesta, and an inner hard, reticulate or transversely grooved sclerotesta; endosperm fleshy, embryo with a straight radicle and flat, foliaceous cotyledons. LECTOTYPE SPECIES: *P. incarnata* L.; see Britton & Brown, Ill. Fl. No. U. S. ed. 2. 2: 565. 1913. (Name from Latin, *passio* (*Christi*), passion or sufferings of Christ, and *flos*, flower, applied from a fancied resemblance of its parts to the implements of crucifixion.) — PASSION-FLOWER.

A genus of about 400 species, primarily of the American tropics, represented in the Western Hemisphere by about 360 species, most of the remaining species occurring in tropical Asia, a few in Australia, Melanesia, and Polynesia, and one on the Mascarene Islands. Harms (1925) subdivided the genus into 21 sections; Killip, however, arranged the American species in 22 subgenera. Six or seven species, representing four subgenera, are indigenous to our area.

Subgenus APODOGYNE Killip (woody vines, petioles 2-glandular, flowers small, in fascicles of 3–6, bracts small, borne near base of peduncle, floral tube patelliform, corona filamentose in two series, operculum plicate, ovary sessile, fruits small, seeds transversely sulcate) includes only *P. multiflora* L., with unlobed, pinnately or subtriplinerved leaves and an anomalous stem structure. The species is mostly West Indian in range (Greater Antilles [except Jamaica] and the Virgin Islands), extending northward on the Florida Keys (Key West to Elliott's Key) to southern peninsular Florida.

Subgenus PLECTOSTEMMA Masters (herbaceous vines, petioles with or without glands, flowers small, peduncles solitary or in pairs, usually 1(rarely 2–10)-flowered, bracts small, scattered [in ours] or wanting, floral tube patelliform [or campanulate], petals sometimes wanting, corona filamentous, in 1 or 2 series, operculum plicate, ovary on a gynophore, fruits small, seeds reticulate or transversely sulcate) includes about 115 species, three of which are indigenous in our area. The very polymorphic *P. suberosa* L. (*P. pallida* L.), $2n = 24$, with undivided to deeply 3-lobed leaves and apetalous flowers, is common throughout tropical America (except the Guianas), and is widely naturalized in the Old World tropics. It occurs on the Florida Keys and in peninsular Florida as far north as the Indian River (Brevard County) in the east, and the mouth of Tampa Bay in the West; it also reaches southernmost Texas (Cameron County). An autotriploid chromosomal race ($2n = 36$) which appeared spontaneously in the wild diploid race has been found by Storey (1950) in Hawaii. *Passiflora sexflora* Juss., with 3-lobed leaves (which often appear almost 2-lobed because of reduction of the middle lobe), glandless petioles, and geminate 2–10-flowered peduncles, is West Indian–Central American in range. It is disjunct southward in Colombia and reaches our area on the Everglade Keys in southern Florida. *Passiflora lutea* L., $2n = 24, 84$, the most northerly of the genus, is distributed throughout our area, extending beyond it westward to Texas, Oklahoma, and Kansas, and northward to southern Illinois, Indiana, Ohio, and Pennsylvania. Recorded chromosome

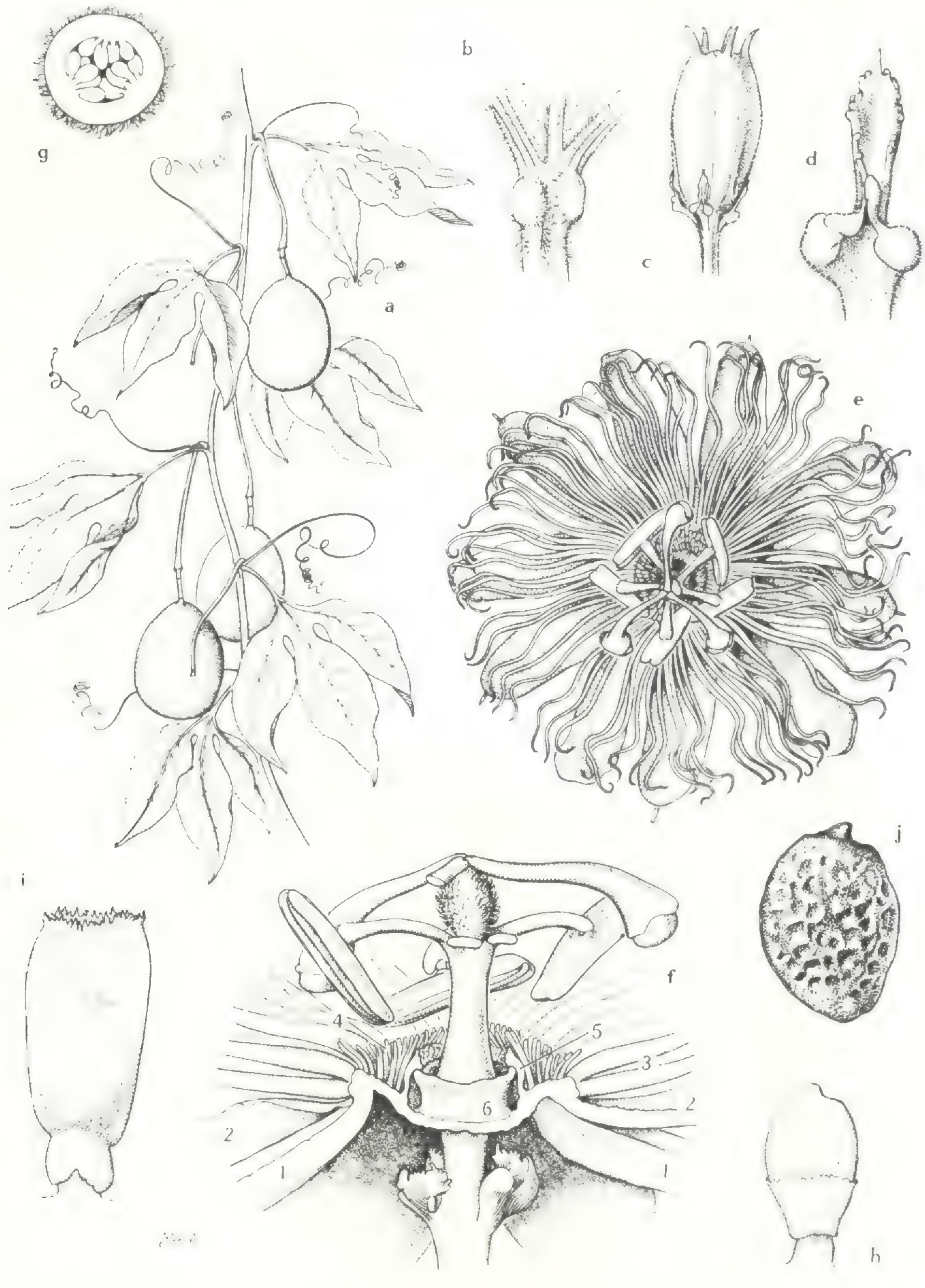

FIG. 1. **Passiflora.** a–j, *P. incarnata*: a, portion of stem with fruits, × ¼; b, summit of petiole with glands, × 3; c, bud with bractlets, × 1; d, bractlet with glands, × 5; e, flower, color pattern omitted, × 1; f, flower, central portion in partial vertical section, two stamens, one style-arm removed, × 2 — note 1-sepal, 2-petal, 3-outer corona, 4-inner corona, 5-operculum, 6-limen; g, ovary, diagrammatic cross section, × 6; h, very young seed with developing aril, × 3; i, older seed with aril, × 3; j, seed with sarcotesta removed, × 4.

counts "indicate that polyploidy exists in this species and suggest that there are intraspecific chromosomal races" (Baldwin). The South American *P. morifolia* Mast. has been reported as naturalized near Clemson, South Carolina (Small, Man. 896. 1933, as "*P. Warmingii* Mast."). The likewise South American *P. gracilis* Jacq. ex Link, $2n = 18, 20$, was introduced into South Carolina (Abbesville County) in the past century.

Subgenus PASSIFLORA (subg. *Granadilla* (Medic.) Mast.) (herbaceous [rarely woody] vines, petioles 2-glandular, flowers generally large and highly colored, solitary or in pairs in the leaf axils, bracts entire or serrulate [or serrate], often large, forming an involucre near the base of the flower, floral tube campanulate to short-tubular, corona filamentous in 3 to several series, operculum nonplicate, ovary stipitate, fruit usually large, seeds reticulate) includes about 100 species, predominantly South American, two in our area. *Passiflora incarnata*, $2n = 18$, with deeply 3–5-lobed glandular-serrulate leaves and large flowers with corniculate sepals and lavender (pink or white) corona, is distributed throughout our area, extending westward to Texas, Oklahoma, and southeastern Kansas, northward to the southern parts of Missouri, Illinois, Indiana, and Ohio and southwestern Pennsylvania; it is introduced and naturalized in Bermuda. The fruits, "maypops," are ellipsoidal, greenish yellow, 3.5–6.0 cm. long; the arils of the seeds ("pulp" of fruits?) are edible. The species is often cultivated elsewhere as an ornamental. *Passiflora pallens* Poepp. ex Mast., with 3-lobed entire-margined leaves, conspicuous foliaceous stipules, large white flowers, and sepals with a foliaceous appendage on the back just below the apex, is known in our area only from a few localities in Dade and Monroe counties in southern peninsular Florida. *Passiflora caerulea* L., $2n = 18$, probably indigenous to Brazil, Uruguay, and Paraguay, is the commonest passion-flower grown as an ornamental in- and or out of doors in both hemispheres. Artificial hybrids between this and several other species are known. *Passiflora edulis* Sims, *P. laurifolia* L., *P. maliformis* L., and *P. quadrangularis* L. (including *P. macrocarpa* Mast.), all $2n = 18$, are extensively cultivated in the tropics for their edible fruits and/or as ornamentals.

Subgenus DYSOSMIA (DC.) Killip (herbaceous vines [or erect shrubs or subshrubs], often with glandular hairs, petioles glandless, stipules usually pinnately cleft or parted, flowers medium-sized to large, bracts pinnatifid to tripinnatisect with filiform gland-tipped segments, floral tube campanulate, corona in 4 or 5 series, operculum nonplicate, fruits medium-sized, seeds reticulate) comprises about 15 species distributed from Brazil to Mexico and the West Indies. *Passiflora foetida* L., $2n = 18, 20, 22$, an extremely polymorphic species including 38 varieties (Killip 1938), ranges throughout the New World tropics, extending as far north as Arizona (var. *arizonica* Killip) and Texas (var. *gossypiifolia* (Desv.) Mast., $2n = 20$). In our area the species (var. *riparia* (C. Wright) Killip) apparently is known only from Fruitland Park, Lake County, Florida, where it was collected by R. N. Jones in 1920. Killip includes "Southern Florida" in the natural range, but the single collection from central Florida suggests

an introduction. The species has been introduced into the tropics of the Old World, where it is now completely naturalized and widely distributed. The unripe fruits are poisonous. [The exclusively South American subg. ASTROPHEA (DC.) Mast. is noteworthy, for, in addition to vines, it also includes tendrilless trees (e.g., *P. arborea* Spreng.) and shrubs (e.g., *P. gigantifolia* Harms).]

The occurrence in the wood of fibriform vessel elements in *Passiflora* (and in some Flacourtiaceae–Paropsieae) presents a notable anatomical peculiarity. The anomalous stem structure of *P. multiflora* probably occurs in some other members of the genus and the family.

Anatomical studies indicate that the floral tube (floral cup) in *Passiflora* is of appendicular origin (except the very base, which is receptacular), involving the fusion of the basal portions of sepals and petals. According to Masters and Puri, the sepals probably are homologous with leaf sheaths, and the dorsal appendages of the sepals (corniculi and the like) are homologous with petioles. The corona and operculum are also appendicular, being outgrowths of the inner wall of the floral tube; the limen, however, probably is staminodial in nature. The parietal placentae of the ovary apparently have been derived from ancestral axile placentae.

Little is known regarding the pollination agents in *Passiflora*, but the following are considered the most probable: bees and other small hymenopters (for subg. PLECTOSTEMMA, sects. *Cieca* and *Decaloba*), large bumblebees, carpenter bees, and large moths (for subg. PASSIFLORA, CALOPANTHUS, DISTEPHANA, and GRANADILLASTRUM), lepidopters (for some species of subg. ASTROPHEA), and hummingbirds (for some species of subg. ASTROPHEA and perhaps subg. TACSONIA and PSILANTHUS, which have long cylindrical floral tubes). Cross-fertilization seems to be the rule, although occasional self-fertilization has been recorded in *P. gracilis*. Self-fertilization is at least in some cases prevented by androgyny (recorded in *P. caerulea* and *P. lutea*, but probably more frequent within the genus) and/or self-sterility (in *P. caerulea*, *P. edulis*, and several other species); *P. mollissima* (HBK.) Bailey, $2n = 18$, is self-fertile.

In the bud both stamens and styles are upright, the anthers being introrse and parallel to the filaments. During anthesis the filaments spread out, taking first a horizontal position, but soon curving down; at the same time the anthers turn around their place of attachment about 90°, becoming perpendicular to the filaments, and finally horizontal and extrorse. Almost simultaneously with the movement of the stamens (or later in protandrous flowers) the styles recurve, and the stigmas are brought to or above the level of the anthers and between them. In this position both anthers and stigmas can be brushed by the back of insect visitors.

Chromosome numbers have been counted in about 20 species, several forms, and five interspecific hybrids. All the species examined (except perhaps *P. foetida*) fit within a polyploid series for which a basic number of six or three has been suggested. (See Storey.) Interspecific hybrids are almost invariably sterile.

The leaves and/or stems, sometimes roots, more rarely fruits and/or

seeds of many species contain various amounts of hydrocyanic acid (cyanogenetic glucoside), and several species are recorded as or suspected of being poisonous, e.g., *P. alba* Link & Otto, *P. caerulea*, *P. Herbertiana* Ker-Gawl. ("pulp" of the fruits strongly cyanogenetic), etc. In *P. alba* another toxic substance, perhaps a toxalbumin, seems present in addition to the hydrocyanic acid. *Passiflora alata* Dryander (subg. *Passiflora*) and its allies contain the bitter (?) principles maracugin (maracujin) and passiflorin. Many species have been recorded as having medicinal properties (antispasmodic, sedative, tonic, anthelmintic, diuretic, emetic, etc.) and are locally used in medicine. Various species are of domestic importance as ornamentals and/or for edible fruits (cf. subg. PASSIFLORA).

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A STUDY OF HYBRIDIZATION IN DOWNINGIA (CAMPANULACEAE)

CARROLL E. WOOD, JR.

EVERY TAXONOMIC STUDY is tentative, and none is to be regarded as final, for each is, instead, one more laborious step toward a greater understanding of living organisms. Each careful investigation provides a new level from which subsequent workers may move forward in the analysis of the complexities and the synthesis of the information about a taxonomic group. Progression is thus by stages in taxonomy, as in other branches of science, although this seems often to be misunderstood by workers in other fields, and perhaps sometimes even by taxonomists. The genus *Downingia* Torr., a western American group of Campanulaceae–Lobelioideae, comprising about a dozen species of small, semiaquatic annuals with colorful, intricately formed corollas, well illustrates this continuing development.

The first species of *Downingia* was described in 1829 from plants grown from seeds collected by David Douglas in what is now Oregon, but only this and one other species were recognized until 1886. Then, from 1886 to 1895, nine new species were described, largely by E. L. Greene, who studied the genus in the field. Subsequently, in 1922, W. L. Jepson published a revision of the species of *Downingia* in California, recognizing only seven, and, in 1937, R. F. Hoover provided a key to the species in that state, including thirteen.

Eventually, in 1941, one hundred and twelve years after the description of the first species, came the first monographic study, that of Rogers McVaugh, which represents a masterful achievement in blocking out the species of *Downingia* on morphological bases. Working entirely from herbarium materials, in which the characteristic details of form and color-pattern of the corolla are largely obscured, it was necessary for McVaugh to treat the genus "exactly as if it were a genus of grasses or of the Compositae, where the distinguishing features are often technical ones and equally often invisible to the unaided eye." This admirable monograph may be modified in details, but the basic alignments will stand. Later (1943), McVaugh himself reduced one species to varietal status. His taxonomic treatment has been followed by Mason (1957), who provided excellent illustrations of most of the taxa, and by Munz and Keck (1959).

With McVaugh's monograph as a firm foundation, the present study was undertaken in the hope of adding something of the biological nature of the species, their chromosome numbers and genetic relationships, and the nature of the interspecific barriers. Annual, easily cultivated in quantity in a small space, with handsome and characteristic corollas, convenient for hybridization studies, and with a manageable number of well-marked species, *Downingia* offers almost as many advantages for a study of living

plants as it does disadvantages in an herbarium study. Begun in California, most of this work has been carried out in greenhouses in Massachusetts and North Carolina with restricted samples of only eight of the species and with no possibility for further field observations. However, the results confirm the taxonomic treatment of McVaugh and show the existence of a pattern of aneuploidy and of strong genetic incompatibilities between species. Since the pressure of other matters has made it impossible to carry this research further, it is presented here, with full recognition of its limitations and gaps, to clear the way for other workers who will undoubtedly solve many more problems, while posing still others. None of these studies of *Downingia* has been complete and final, but each is a step toward the continuing taxonomic goal of knowledge and understanding of plants.

Begun in the native haunts of *Downingia*, but carried out mostly on the opposite side of the continent, this work was possible only through the interest and help of friends and colleagues. I can not here detail the encouragement, advice, materials, or help which each has generously given, but I want to express my sincere appreciation to all of the following for their assistance: R. C. Bacigalupi, L. Constance, R. W. Holm, C. E. Kobuski, J. Kucyniak, Estella Leopold, C. MacMillan, Phyllis Gardner MacMillan, R. McVaugh, C. T. Mason, L. I. Nevling, Jr., M. A. Nobs, J. E. O'Connell, J. A. Rattenbury, R. C. Rollins, O. T. Solbrig, W. G. Solheim, G. L. Stebbins, Jr., the late A. N. Steward, W. H. Wagner, Jr., A. R. Kruckeberg, and R. L. Wyatt. *Figure 8* was drawn by Margaret F. Schroeder, of Cambridge, Massachusetts, from a Kodachrome slide and from preserved flowers. The manuscript could not have been completed without the able help of Mrs. Gordon W. Dillon.

METHODS

The first collections studied were made in California in the spring of 1949 by friends at the University of California or by myself, and a few hybridizations between wild plants brought into the greenhouses at Berkeley were tried at that time. Subsequently, a number of botanists kindly collected and forwarded seeds of various species. Attempts were made to grow and observe the crosses made in 1949, as well as other available collections, at the Biological Laboratories, Harvard University, Cambridge, Massachusetts, in the spring of 1950 and again in 1951. In the next three years, plantings at the University of North Carolina, Chapel Hill, were successful only in 1953; those in 1952 and 1954 mark unfortunate breaks in the data, for all failed, almost none of the seeds germinating (for causes unknown).

Seeds of *Downingia* were sown in February in 3-inch pots or 6-, 7-, or 9-inch azalea pots or bulb pans, in a more or less standard sand-soil-compost mixture. The sifted, firmly packed soil was covered with a thin layer of very fine soil on which the minute seeds were either scattered or placed

individually. A light dusting of sifted soil was added and the surface lightly tamped. The pots stood in saucers or pans of water and were kept constantly wet.

A large number of plants of *Downingia* can be grown in a single pot, allowing ready comparison within small populations. Under such conditions, individual plants do not reach the size or vigor which may be seen under favorable conditions in the wild or when grown singly in the greenhouse, but limitations of space necessitated the arrangements adopted.

In Cambridge six hours of additional light from two 1000-watt bulbs suspended over the greenhouse bench were used in 1951. The effect of the supplemental light will be seen under each species in the length of time required for flowering in this year in comparison with 1950 and 1953.

Sandwiched between other more pressing work, chromosome counts could not always be made at the proper time and were not obtained for all of the collections grown. The counts recorded, all meiotic, showed a pattern of aneuploidy from 11 pairs to 12 and to 10, 9, and 8. These chromosome numbers are given under the species concerned and are summarized in the crossing diagram and discussion toward the end of the paper. Meiosis occurred when the apparent flower bud (not including the pedicel-like ovary) was about 1 mm. long. The best results were obtained when the first buds were being produced in a population; at that time it was possible, with a little patience over a period of a few days, to obtain satisfactory meiotic material. Later on, after the plants were larger, I found it difficult to select buds which were of the proper age.

The material gave good results with a modified Carnoy's fixative (4 parts chloroform: 3 absolute ethyl alcohol: 1 glacial acetic acid) and proprionocarmine. Slides were made permanent with a modification of Bradley's vapor transfer method (Stain Tech. **23**: 41–44. 1948). Documenting herbarium specimens are in the Gray Herbarium.

The pollen discharge device of *Downingia* (see below) makes hybridization relatively easy. The ovary of a flower was held between forefinger and thumb and the anther tube grasped carefully with forceps and tweaked off. In most instances a clean separation from the filament tube could be obtained and the anthers pulled away, leaving the protruding style with the rudimentary stigmas. When the stigmas matured, pollination of the emasculated flower was accomplished easily with a spear-pointed needle which was used to depress the anther bristles and to collect the out-pouring of pollen. Pollen was then transferred to the appropriate stigma, the needle dipped in 70 per cent alcohol, the pollinated flowers marked with jeweler's tags, and the fruits allowed to mature. (Since the bright yellow pollen is rather powdery, some stray contamination may have come about through the methods used, for the small size of the plants, their closeness in the pots, and the importance of the ovary in the photosynthesis of the plant all precluded any sort of hermetic bagging. Such seedlings were easily recognized in interspecific crosses but could be a serious source of error in crosses involving races of a species. Nonhybrid seedlings of this kind are given for each of the interspecific crosses.) In *Downingia cuspi-*

data and *D. bicornuta* var. *bicornuta* the capsules tended to dehisce almost immediately upon maturity, necessitating prompt gathering. In other species most capsules on a single plant could be gathered at the same time and placed in individual coin envelopes. Each capsule involving an interspecific cross was split lengthwise with a needle and the number of seeds and/or the condition of aborted ovules recorded.

More than 900 cross-pollinations were effected between the species assembled, the seeds sown, and the results tabulated. These are summarized under each of the species and in *figure 13*, which shows all crosses attempted and the several categories of results, as well as chromosome numbers.

GENERAL OBSERVATIONS

The twelve species of *Downingia* are all low annuals admirably adapted to the climatic conditions of the western United States, especially that part in which the Mediterranean type of climate, with its wet, cool winters and hot, dry summers, prevails. All are associated with moisture, and most are plants either of vernal pools or vernally wet soils. Growth is slow during the winter. With lengthening days, rising temperatures, and drying of the vernal pools, the rate of growth increases and the plants come rapidly into flower and set and mature seeds before the drying of the soil kills the parental plant. Numerous minute, fusiform seeds (to 150 or more) are borne on axile or parietal placentae in elongate 1- or 2-locular cylindrical capsules, which in some species (e.g., *D. cuspidata*) open almost immediately upon maturity by longitudinal splits, but in others (e.g., *D. ornatissima*) appear to be almost or quite indehiscent. In spite of their small size the seeds of some species, particularly those of habitats with the hottest, driest summers (e.g., *D. concolor*, *D. cuspidata*, *D. ornatissima*, *D. pusilla*) appear to be relatively drought resistant and may retain their germinability over a period of years. Those of cooler and moister habitats (e.g., *D. montana*, *D. yina* var. *major*, *D. elegans*) appear to be viable a much shorter length of time.

In nature, the seeds presumably germinate in fall or winter, either on wet soil or under water. The seedling shows an adaptation characteristic of a number of aquatics or plants of seasonally wet habitats. (Cf. *Drosera*, *Sarracenia*, *Pinguicula*, and many aquatics illustrated in W. C. Muenscher, Aquatic Plants of the United States [1944].)

In about five to seven days (in the greenhouse), the hypocotyl pushes out of the micropylar end of the seed and comes into contact with the soil. The radicle remains quiescent until the development of a ring of long root hairs at the base of the hypocotyl provides an anchoring attachment. The radicle then begins to grow, and, as the primary root elongates, the usual root hairs are formed.

The hypocotyl then elongates, becoming upright and green. The linear-lanceolate cotyledons gradually emerge, but remain pressed together, the tips being held within the seed coat. With the beginning of growth of the

plumule, the cotyledons may expand or may be held together permanently by the seed coat. Under favorable conditions growth proceeds rapidly. As with many marsh or aquatic plants, the stems are equipped with large gas channels which extend into the roots. Axillary branches may occur from the cotyledons upward, and adventitious rooting may occur at the nodes. A burst of growth appears in connection with the formation of the flower buds, which are solitary and sessile in the axils of bractlike leaves (the first appearing in the axil of the fifth to tenth or fifteenth leaf above the cotyledon, depending upon the species). These upper leaves and especially the elongated cylindric ovaries (which may easily be mistaken for pedicels) must account for much of the photosynthetic area of the plant.

In culture, flowering may occur in *D. pusilla* (the most reduced species) in about 35 days from the time of planting, or in about 45–56 days in most species, or may require some 70 in *Downingia bicornuta* var. *bicornuta*. The flowers are inverted in anthesis by tortion of the ovary, the apparent lower lip being morphologically the upper one. The flowers, with their elaborate and colorful corollas, obviously are adapted to insect pollination. The "lower" lip is more or less highly modified as a "landing platform" and is marked with characteristic patterns of blue to violet, white, yellow to green, and dark purple. The androecium is equally specialized, reserving the pollen until activated by an insect visitor. Most of the species (with the exception of the diminutive *Downingia pusilla* which seems to be self-pollinated) are normally outcrossing, but are self-compatible and may, under some circumstances (see below), be self-pollinated. Seedlings obtained from self-pollination in *D. insignis* and *D. pulchella* show variation in color pattern, suggesting the heterozygosity associated with outcrossing. No evidence of apomixis was found in the present investigation, and none of the cultures set seeds without pollination.

Androecium. The androecium of *Downingia* is a characteristic and highly specialized one, modified along the same lines as that of many of the members of Campanulaceae–Lobelioideae and resembling especially those of its nearest relative, *Porterella carnulosa* (Hook. & Arn.) Torr. (see Mason, 1957, *fig. 344*), and of *Isotoma axillaris*, described recently by Melville (1960). The five stamens are united around the style, the filaments forming a tube and the five anthers a more or less cylindric anther tube oriented at various angles to the filament tube. (See *figs. 1, 8*; also McVaugh, 1941, *figs. 1–3, 5, 6, 10*, and Mason, 1957, *figs. 331–340.*) The three larger anthers are uppermost, the tips curving downward and inward to those of the two shorter and smaller lower anthers and forming a mouth-like opening. Each of the two smaller anthers is tipped by a few forwardly directed short hairs and by a conspicuous flexible, flap-like bristle which projects forward at the base and then usually downward. The bases of the two bristles and the tuft cover the opening between the anthers, preventing the loss of pollen which is shed inwardly into the common cavity of the anther tube. When one or both of the bristles are

FIG. 1. Stamens of species of *Downingia*, in lateral view to show differences in size, angle of anther tube to filament tube, and length and position of anther bristles. Numerals following the name refer to populations listed under the species. All figures × 6 or 12. a–c, *D. bicornuta* var. *bicornuta* (30); d, e, *D. bicornuta* var. *picta* (40); f, *D. bicornuta* var. (2674), diagrammatic; g, h, *D. concolor* var. *concolor* (34); i, j, *D. cuspidata* (31); k, l, *D. elegans* var. *brachypetala* (39); m, n, *D. insignis* (14); o, p, *D. ornatissima* var. *ornatissima* (36); q, r, *D. ornatissima* var. *eximia* (28); s, t, *D. pulchella* (26).

pushed backward by a pollinator, the opening is uncovered and a quantity of powdery pollen bursts forth in a stream, dusting the insect. Subsequent displacements produce additional quantities of pollen.

The impetus for the pollen movement is provided primarily by the growth of the style. At the time of shedding of the pollen, the style is about as long as the filament tube, but the two stigmatic lobes are rudimentary and are tightly appressed to each other, the two occupying about the same diameter as the style. Immediately behind them is a ring of several ranks of stylar hairs. With the continuing elongation of the style, the hairs act as a plunger, putting the pollen ahead under pressure and pushing it against the tips of the three upper stamens, so that it pours out, as though a valve were opened, when the anther bristles are depressed. A second source of pressure on the pollen may possibly come from the shrinking and drying of the tough outer walls of the anthers. The growth of the style continues, and, when the undeveloped stigmatic lobes push through and beyond the anther tube, they expand rapidly, separating, recurving, and maturing. (See Mason, 1957, *fig. 334f.*)

The flowers are thus strongly proterandrous, and self-pollination usually cannot occur. Exceptionally, however, in all of the species studied here, the style may fail to push through the anther tube, with the result that the stigmas expand within the tube and self-pollination occurs. In the single collection grown of *Downingia pusilla*, self-pollination of this type appeared to be the rule, for the stigmas were seldom seen to protrude from the anther tube, and, in contrast to the other species, in greenhouse culture plants of *D. pusilla* always set many seeds whether or not artificial pollination was attempted. (Apomixis, with the possible exception of pseudogamy, may be ruled out here, for emasculated flowers of *D. pusilla* did not set seeds.)

In his monograph of *Downingia*, McVaugh found that the androecium furnishes some of the most useful taxonomic characters for the identification of herbarium specimens (in which the corollas are almost always deformed and faded). Although flower size may vary greatly with the size and vigor of the plant, the androecium is relatively constant quantitatively and has a characteristic range in length. It is usually distinctive in shape of the anthers, the angle of anther tube to filament tube, the anther pubescence, the length and shape of the bristles, and the degree of exsertion of the anthers from the corolla tube. Such characteristics, combined with the elaborately formed and colored corollas, suggest specific pollination agents, or at least different sizes of agents. However, only a single field observation is available. (See *Downingia concolor.*)

The pollen discharge device of *Downingia* is more advanced than that of *Lobelia* and some other Lobelioideae in the elaboration and specialization of the two trigger bristles, the bases of which close the anther tube. In several species of *Lobelia* in which I have tested this mechanism, the bristles are lacking and the opening is closed by the two tufts of forwardly directed hairs which also act as the trigger device, releasing the pollen when pushed downward. In the eastern United States, the ruby-throated

hummingbird regularly trips the device of *Lobelia cardinalis* and may be seen with the top of the head yellow with pollen, while honey bees visiting *L. siphilitica* deliberately manipulate the discharge hairs and collect and carry away in their pollen baskets the bluish-gray pollen with which they are then dusted. However, the bristles of *Downingia* and *Porterella* would seem to make for a somewhat more efficient and sensitive mechanism.

OBSERVATIONS ON THE SPECIES

The data given here include notes which have accumulated in the course of growing and attempting to hybridize the eight species. For ease in consultation, the species are arranged in alphabetical order. Under each will be found observations (intended only to supplement those of McVaugh [1941] and the excellent drawings in Mason [1957]) on color patterns and morphology of the flowers, documenting data on the collections grown, summaries of the crosses attempted with other species, chromosome counts, and miscellaneous notes and comments which bear on the biology or taxonomy of the species. In all crosses the seed parent is given first. The hybrids of *Downingia insignis* and *D. pulchella* are treated separately in a following section.

Downingia bicornuta Gray var. bicornuta

FLOWER MORPHOLOGY AND COLOR: See *fig. 2* for conformation and general color pattern of corolla; see also McVaugh (1941, *figs. 4, 5*, and p. 27), Mason (1957, p. 755). Lower lip of corolla nearly plane, not concave as in var. *picta*, the outer portion blue-violet (Bradley's violet [Ridgeway]), the central area white with two green to sulfur-yellow spots (these usually confluent as single patch) extending to the mouth of the corolla tube; upper lobes erect or reflexed, divergent or overlapping, blue-violet without and within; corolla tube blue-violet, darker on the upper side, the lateral walls with or without violet veining (this inconspicuous on account of the darker ground color); lower side of tube blue-violet within two-thirds of way from base, then with two elongated green or yellow spots or streaks (these visible on the outside) banded with reddish purple at either end, then with a band of violet, and finally with a deep violet band across the front of 2 of 4 hornlike projections at the mouth of the tube, the deep violet sometimes extending into the tube; hornlike projections shorter than in var. *picta*, erect and not curving outward. Corolla tube 5–6.1 mm. long from base to upper sinus, (3.8–)4.8–6.2 mm. long to lateral sinus in fresh material (*vs.* 2.5–4.5 mm. in dried material studied by McVaugh). Anthers not exserted from corolla tube or only tip exserted; anther tube not at an angle to filament tube; anther bristles twisted, short, 0.6–1.5 mm. long. (See *fig. 1a–c.*)

COLLECTION GROWN: 30, from Boggs Lake, Lake Co., Calif., *Estella Leopold*, 31 May 1949 (plants pollinated in wild, seeds matured in greenhouse).

CROSSES ATTEMPTED:

30 × *D. concolor* (34, 87): 133 seeds from 5 capsules, 77 white or pale green lethals, 21 nonhybrids; reciprocal, 65 seeds from 25 capsules, 2 white lethals, 45 nonhybrids.

30 × *D. bicornuta* var. *picta* (40): 620 seeds from 9 capsules, green and vigorous hybrid seedlings flowering in about 56 days (1953); reciprocal (20 capsules, seeds not counted) equally successful; F_1 apparently fertile but F_2 lost in 1954.

30 × *D. ornatissima* (28, 36): 14 seeds from 6 capsules, 2 white lethals, 6 nonhybrids; reciprocal (27, 28, 36 × 30), 235 seeds from 20 capsules, 15 white lethals, 62 nonhybrids.

30 × *D. cuspidata* (33): 3 seeds from 4 capsules, 1 nonhybrid; reciprocal, seeds aborted near maturity, did not germinate or were lethal (in 33 × 30, no seeds from 15 capsules; but 105 seeds from 1 capsule gave 18 nonhybrid seedlings; in 31 × 30, 175 seeds from 7 capsules, about one-half of these planted, 16 white or yellowish lethals, 26 nonhybrids).

30 × *D. pulchella* (26): 49 seeds from 5 capsules, no hybrids, 38 nonhybrids; reciprocal, 21 seeds from 10 capsules, no hybrids, 29 nonhybrids.

30 × *D. insignis* (14): 13 seeds from 4 capsules, no hybrids, 12 nonhybrids; reciprocal, 79 seeds from 13 capsules, no hybrids, 38 nonhybrids.

30 × *D. elegans* var. *brachypetala* (39): 8 seeds from 3 capsules, no hybrids, 1 nonhybrid; reciprocal, 24 seeds from 12 capsules, no hybrids, 1 nonhybrid.

CHROMOSOMES: $n = 11$ (metaphase, anaphase II) in population 30; meiosis regular.

Plants developed relatively slowly, beginning to flower in 69 days in 1950, 64–70 days in 1951. The flowers were without the curious odor of var. *picta*. This collection is the rather large-flowered, slow-maturing northern plant which extends from California into Oregon, Nevada, and Idaho.

Hybrids between vars. *bicornuta* and *picta* were green, vigorous, and apparently quite fertile, beginning to flower in 56 days in 1953. The color pattern of the corolla was like that of var. *bicornuta*, but the corolla tube was shorter and the anther bristles longer. An F_2 planted in 1954 failed, along with all other seeds planted that year. See also var. *picta* below.

Downingia bicornuta var. picta Hoover

FLOWER MORPHOLOGY AND COLOR: See *fig. 2* for conformation and general color pattern of corolla; see also McVaugh (1941, *fig. 6* & p. 27), Mason (1957, *fig. 335a, b*). Outer portion of concave lower lip of corolla violet, central area white with a central yellowish-green spot; upper lobes reflexed or erect, violet, paler at the base; corolla tube conspicuously reticulate within, with deep violet veins on a paler background, the upper side of the tube usually greenish or brownish for a distance of about 1–1.5 mm.; lower side of corolla tube zoned with purple at base, white with two green lines in the median portion, and purple at the distal end, the purple extending onto 4 hornlike projections at the mouth of the tube; exterior

of corolla tube light reddish purple (much paler than in var. *bicornuta*), the reticulations conspicuous, the tube often greenish distally; hornlike projections longer and more conspicuous than in var. *bicornuta*, curving outward, purple, the two central darker because of the extension of the greenish-yellow patch in center of lip over them. Corolla tube 2.4–3.1 mm. long from base to upper sinus, 2.0–2.9 mm. long to lateral sinus (vs. 1.5–2.6 mm. at lateral sinuses in dried material studied by McVaugh). Anthers usually exserted from corolla tube for almost the full length of the anther tube; anther tube at an angle to filament tube. (See *fig. 1d,e.*)

COLLECTIONS GROWN:

40, from 2 mi. n. of Sheldon, Sacramento Co., Calif., *G. L. Stebbins, Jr.*, 20 May 1950 (seeds).

46, from 3.5 mi. n. of Snelling on La Grange Road, Merced Co., Calif., *R. C. Bacigalupi*, 22 April 1951 (seeds).

CROSSES ATTEMPTED:

40 > *D. bicornuta* var. *bicornuta* and reciprocal: good seed-set, green and vigorous hybrids of intermediate morphology. (See var. *bicornuta* above.)

40 × *D. concolor* var. *concolor* (34): 22 seeds from 2 capsules, no hybrids, 11 nonhybrids; reciprocal, 61 seeds from 14 capsules, 7 yellowish lethals, 13 nonhybrids.

40 × *D. ornatissima* (28, 42): 26 seeds from 5 capsules, no hybrids, 10 nonhybrids; reciprocal (with 27, 28, 36, 42), 214 seeds from 25 capsules, 7 white lethals, 35 nonhybrids.

40 × *D. cuspidata* (29, 31): 6 seeds from 2 capsules, none germinating; reciprocal (with 31), 397 seeds from 9 capsules, 78 white or very pale green lethals, 106 nonhybrids.

40 × *D. insignis* (14): not attempted; reciprocal, 18 seeds from 5 capsules, no hybrids, 10 nonhybrids.

40 × *D. elegans* var. *brachypetala* (39): 13 seeds from 6 capsules, no hybrids, 5 nonhybrids; reciprocal not attempted.

CHROMOSOMES: $n = 11$ (metaphase I, anaphase I, metaphase II) in population 40; meiosis regular.

Plants developed rapidly, the first flower bud located in the axil of the fifth leaf above the cotyledons, meiosis occurring in about 36 days and flowering in 50 days in 1951, 53 days in 1953, the first flowers opening two weeks ahead of var. *bicornuta* (cf. McVaugh, 1941, pp. 28, 30). The flowers had a strong "mousy" odor quite different from that of var. *bicornuta* or any of the other species grown.

The flowers of *Downingia bicornuta* var. *bicornuta* and var. *picta* are so different, when seen on the living plant, that on morphological grounds one could well deduce that two species are involved. The corollas differ in color pattern, shape of the lobes and length of the tube, and the androecia in length, angle of anthers to filament tube, degree of exsertion of anthers, and length of the paired twisted bristles. In addition, var. *picta* begins to flower earlier, an adaptation probably related to its restriction to the Central Valley of California. However, on the basis of the twisted bristles,

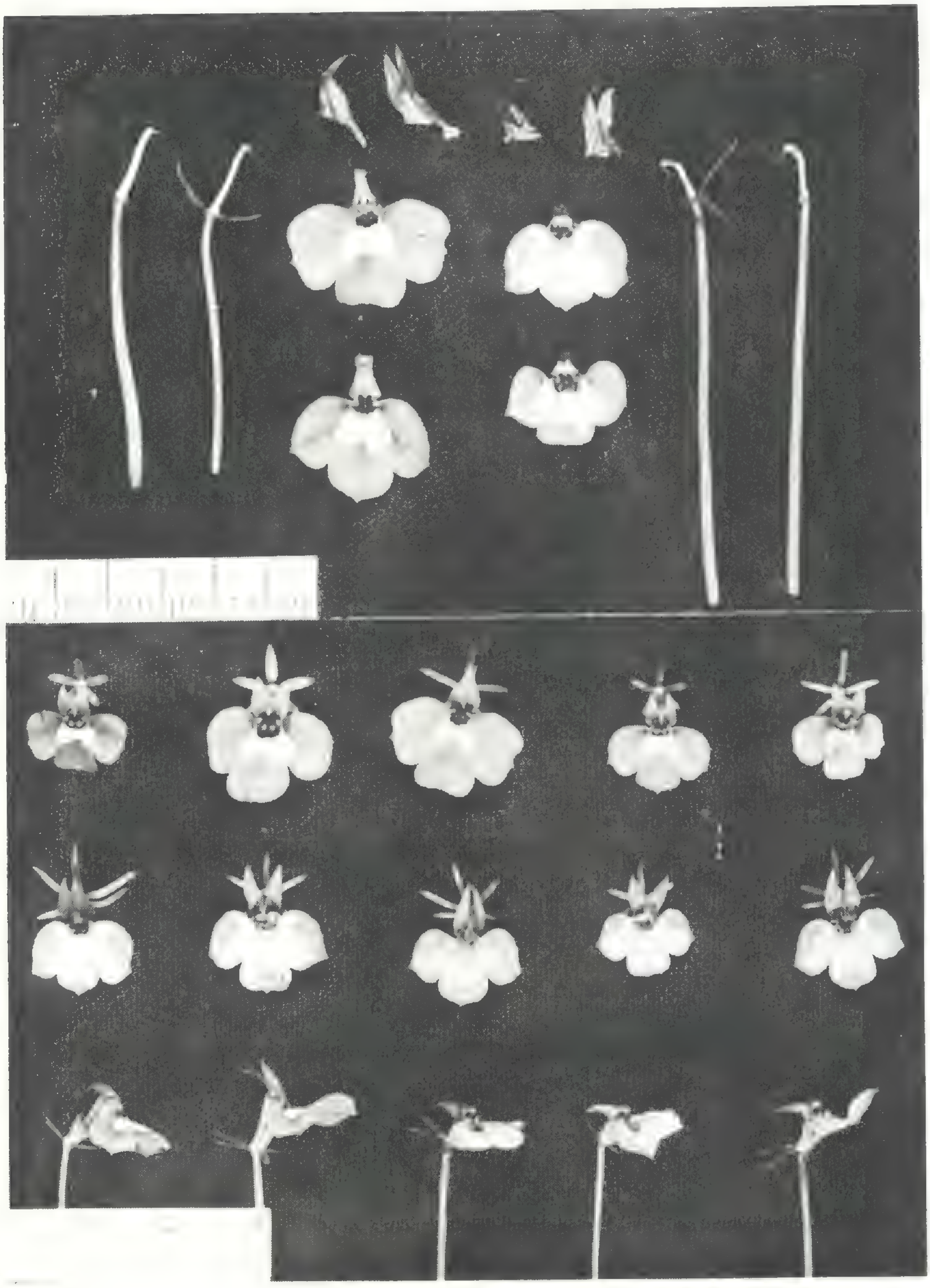


FIG. 2. Flowers of *Downingia bicornuta* vars. *bicornuta* and *picta*. Above: left, var. *bicornuta*, androecium and portion of ovary, upper corolla lobes, lower corolla lobes; right, var. *picta*. Below: top row, var. *bicornuta*; center row, var. *picta*; bottom row, two flowers of var. *bicornuta* (left), three of var. *picta*.

the corolla tube bearded within on the lower side, and the four conspicuous hornlike projections on the lower lip at the entrance to the corolla tube, as well as the occurrence of occasional apparent intermediates in the Sacramento Valley where the ranges of the two appear to overlap, McVaugh treated both as components of one species. The chromosome numbers and crossing evidence are entirely in accord with this disposition.

Downingia bicornuta var. [with short anther bristles and corolla tube]

FLOWER MORPHOLOGY AND COLOR: Appearing to be a small-flowered form of var. *bicornuta*; sepals and formation and color pattern of corolla as in var. *bicornuta*, but the corolla tube somewhat paler. Corolla tube short, 3.0–4.5 mm. long from base to upper sinus, 2.7–4 mm. long to lateral sinus in fresh material. Anthers as in var. *bicornuta*, with short, straight or twisted bristles, the anther tube not exserted from the corolla tube and not at an angle to the filament tube; filament tube ca. 2.6 mm. long. (See *fig. 1f.*)

COLLECTION GROWN: in alkaline pools, 2 mi. w. of Tranquility Junction on State Highway 180, Fresno Co., Calif., *Bacigalupi, Wiggins & Ferris 2674*, 29 July 1941 (GH) (flower and fruit).

CROSSES ATTEMPTED: This collection was crossed with vars. *picta* (46) and *bicornuta* (30) in 1953. Seed-set apparently was normal, but the hybrid seed planted in 1954 failed, along with all other seeds sown that year.

CHROMOSOMES: $n = 11$ (metaphase–anaphase I); meiosis regular.

The seeds from which this culture was grown came from a then ten-year-old specimen in the Gray Herbarium. The seeds, which bore faint longitudinal cellular markings, germinated readily in about 8 days. The plants developed rapidly, meiosis occurred about 34 days after sowing and flowering began in about 55 days in 1951 (sown in mid-April) or 50 days in 1953 (sown in late February).

This plant, which indicates the need for further study of variation in *Downingia bicornuta*, is undoubtedly closely allied to var. *bicornuta*, which it resembles in the conformation and coloration of the corolla, in the sepals, in the included anthers, in the straight filament-anther tube, and in the short anther bristles. It differs, however, in the short corolla tube (intermediate in length between the cultures grown in vars. *bicornuta* and *picta*), the filament tube (even shorter than that of var. *picta*), and in the time of flowering. It thus combines some features of vars. *bicornuta* and *picta*, but the uniformity of the population grown, the short filament tube, and the short bristles suggest at least that this is not of immediate hybrid origin. The geographical distribution remains to be determined, but it may be suspected of being a low-altitude, rapidly maturing form of at least the southern part of the Central Valley of California. Collections from the Central Valley which appear to be var. *bicornuta* should be examined critically.

This collection was determined by McVaugh as *Downingia bella* Hoover, a species which was imperfectly known to him and one of which I have seen only scanty herbarium material. (See Mason, 1957, p. 754, for illustration of *D. bella*.) The determination is easily understandable, for, in the herbarium specimen, the details of the corolla are quite obscured and the anther bristles are not the characteristically twisted ones of *D. bicornuta*. However, whatever the identity of *D. bella*, a plant which McVaugh thought to be related to *D. concolor*, the present plant is clearly allied to *D. bicornuta*, with both of the recognized varieties of which it is presumably interfertile.

Downingia concolor Greene var. concolor

FLOWER MORPHOLOGY AND COLOR: See McVaugh (1941, *fig. 12* & pp. 18–21), Mason (1957, pp. 752, 755). Corolla pale to bright blue, the lower lip with a central white area and, at the mouth of the corolla tube, with a 2-lobed to w-shaped to almost square velvety, dark-violet spot covering two low ridges, each of which sometimes bears a streak of yellow within the mouth of the tube; white of the lip sometimes reduced or lacking, the whole lip then blue, the purple spot then completely obscuring the yellow streaks; corolla tube narrowly funnel-shaped, the lower side reddish violet from base to middle (or the entire length in dark flowers), the distal portion light blue to almost white.

COLLECTIONS GROWN:

15, from dry, hard adobe, roadside ditch, ca. 10 mi. s. of Dixon, Solano County, Calif., *C. E. Wood 7614*, 16 April 1949 (plants in flower; growing with *D. insignis*).

20, in vernal pools in meadow, ca. 2¼ mi. ne. of Middletown, Lake Co., Calif., *C. E. Wood 7620*, 28 April 1949 (plants in flower).

34, from near Dixon, Solano Co., Calif., *M. Nobs*, May 1949 (living plants).

87, a population originated in the greenhouse through crossing of 15 × 20 in May, 1949, before any chromosome numbers had been determined.

1170, growing in Middletown Meadow (Skaggs Ranch or Bar X Ranch), 3 mi. e. of Middletown on Highway 53, Lake Co., Calif., *A. R. Kruckeberg*, 2 July 1949.

INTERSPECIFIC CROSSES ATTEMPTED:

34, 87 × *D. ornatissima* (27, 35, 36, 42): 47 seeds from 28 capsules, 1 white lethal, 25 nonhybrid seedlings; reciprocal (27, 28, 35, 36 × 34, 87), 129 seeds from 35 capsules (43 from 1 capsule, 23 from another), 14 white lethals, 52 nonhybrids.

34, 87 × *D. bicornuta* var. *bicornuta* (30): 65 seeds from 25 capsules, 2 white lethals, 45 nonhybrids; reciprocal, 133 seeds from 5 capsules, 73 white to pale green lethals, 22 nonhybrids.

34 × *D. bicornuta* var. *picta* (40): 61 seeds from 14 capsules, 7 very pale, yellowish lethals, 13 nonhybrids; reciprocal, 22 seeds from 2 capsules, no hybrids, 11 nonhybrids.

15, 34, 87 × *D. cuspidata* (29, 31, 33): 37 seeds from 23 capsules, 4 pale green lethals, 22 nonhybrids; reciprocals (31, 33 × 15, 20, 34, 87), 188 seeds from 27 capsules, 30 white lethals, 64 nonhybrids.

34 × *D. pusilla* (2063): 71 seeds from 2 capsules, 48 weak and nearly white lethals, some surviving almost 4 weeks.

15, 20, 34, 87 × *D. pulchella* (25, 26): 27 seeds from 18 capsules, no hybrids, 17 nonhybrids; reciprocal (25, 26 × 15, 34, 87), 86 seeds from 16 capsules, 1 white lethal, 67 nonhybrids.

34, 87 × *D. insignis* (14): 32 seeds from 21 capsules, no hybrids, 25 nonhybrids; reciprocal (14 × 15, 20, 34, 87), 131 seeds from 40 capsules, 3 white or very pale green lethals, 45 nonhybrids.

34 × *D. elegans* var. *brachypetala* (39): 99 seeds from 9 capsules, no hybrids, 90 nonhybrids; reciprocal, 34 seeds from 5 capsules, no hybrids, 28 nonhybrids.

CHROMOSOMES: $n = 8$ (metaphase II) in population 34; $n = 9$ (late diakinesis to metaphase I) in population 1170; meiosis regular in both.

Plants matured rapidly, flower buds appearing in the axil of the seventh leaf above the cotyledons. Meiosis occurred in about 33 days after planting in 1951, and the first flowers opened in 55 days in 1950, 43–49 days in 1951, and 53 days in 1953.

The presence of two chromosome numbers (eight and nine) in two populations (34, 1170) of this species in northern California is of special interest. The meiotic behavior of a hybrid between these two races should provide a valuable clue to the way in which aneuploid repatterning of the chromosome complement has proceeded in the genus. Chromosome counts were not obtained on cultures 15 and 20 which are from approximately the same areas as are the 8- and 9-chromosome cultures (34 and 1170 respectively) and which might well have the same number of chromosomes as those collections. Wild plants from which cultures 15 and 20 were derived were crossed in California in 1949, long before any chromosome counts had been made. The resulting population (87) appeared to be fully fertile, and estimates, confusing at the time, of nine (definite) and eight (tentative) were both obtained, but these data are anything but unequivocal. No meiotic irregularities were seen, and one count of 1000 pollen grains showed 98.1 per cent stainable.

Another relationship which should be investigated is that of *Downingia concolor* var. *brevior* McVaugh, known only from San Diego County, California, and distinguished by its shorter and readily dehiscent capsules, to these more northern plants. Also of interest is the relationship of *D. concolor* to *D. bella* Hoover, which it resembles in a number of features.

This is the only species in which I have observed pollination in the wild. In Lake County, California, a small bee, unfortunately not captured, was seen visiting successive flowers (population 20). Pollen was being ejected on the face of the bee above the mouthparts, suggesting that the positions of the anthers in the various species may result in the deposition of pollen on specific parts of the pollinator's body.

Downingia cuspidata (Greene) Greene ex Jepson

FLOWER MORPHOLOGY AND COLOR: See McVaugh (1941, p. 31), Mason (1957, p. 759). Lower lip of corolla nearly plane, the lobes sky-blue to pale blue (or the blue varyingly restricted, in some plants only the very tips bluish), occasionally violet or pink (or anthocyanin sometimes entirely suppressed), the central area white with a two-lobed yellow spot covering two inconspicuous, low, mound-like ridges at the entrance to the corolla tube; upper lobes correspondingly blue, violet, or pink, usually somewhat darker than lower lobes, erect; corolla tube narrow, pale, unmarked, except for the tip of the yellow spot which extends to within the entrance; mouth of corolla tube narrow, mostly filled by the slightly exserted anther tube.

COLLECTIONS GROWN:

29, in one of four vernal pools about 1.5 feet deep with bare (dry) bottom and scattered plants of *Eryngium*, ca. 2 mi. e. of Keystone, Tuolumne Co., Calif., *C. E. Wood 7629 & C. T. Mason*, 9 May 1949 (only this species present, in fruit; absent in two shallower adjoining pools).

31, in very dry, very hard clay in three dry vernal pools in blue-oak grassland, ca. 3 mi. w. of Coarse Gold, Madera Co., Calif., *C. E. Wood 7631 & C. T. Mason*, 10 May 1949 (most plants with mature seeds, a few, including one pink and one violet, in flower).

33, in vernal pools along highway in bottomlands near a creek, ca. 1.2 mi. w. of Chinese Camp, Tuolumne Co., Calif., *C. E. Wood 7633 & C. T. Mason*, 10 May 1949 (fruiting in a dry pool, but flowering in wet areas).

47, from 3 mi. n. of Snelling on La Grange Road, Merced Co., Calif., *R. C. Bacigalupi*, 22 April 1951 (seeds).

INTERSPECIFIC CROSSES ATTEMPTED:

31, 33 × *D. concolor* var. *concolor* (15, 20, 34, 87): 188 seeds from 27 capsules, 30 white lethals, 64 nonhybrids; reciprocal (29, 31, 33 × 15, 34, 87), 37 seeds from 27 capsules, 4 pale green lethals, 22 nonhybrids.

31, 33 × *D. ornatissima* (27, 35, 36): 536 seeds from 33 capsules, 136 white lethals, 78 nonhybrids; note especially 31 × 27, 293 seeds from 6 capsules, 112 white lethals, 48 nonhybrids; reciprocal (with 27, 28, 35, 36), 27 seeds from 41 capsules, no hybrids, 10 nonhybrids.

31, 33 × *D. bicornuta* var. *bicornuta* (30): seeds aborted near maturity, did not germinate or were white lethals (in 33 × 30, no seeds from 15 capsules, but 105 seeds in one capsule gave 18 nonhybrid seedlings; in 31 × 30, 175 seeds from 7 capsules, about one-half of these planted, 16 white or yellowish lethals, 26 nonhybrids); reciprocal (33 × 30), 3 seeds from 4 capsules, no hybrids, 1 nonhybrid.

31 × *D. bicornuta* var. *picta* (40): 397 seeds from 9 capsules, 78 white or very pale green lethals, 106 nonhybrids; reciprocal (40 × 29, 31), 6 seeds from 2 capsules, none germinated.

31 × *D. pusilla* (2063): 39 seeds from 2 capsules, no hybrids, 20 nonhybrids; reciprocal (with 29, 31), plants not emasculated, 61 seeds from 5 capsules, no hybrids, 47 nonhybrids, two capsules, each with 25 flat and twisted seeds aborted near maturity.

31, 33 × *D. pulchella* (26): 117 seeds from 20 capsules, 5 white or pale green lethals, 33 nonhybrids; reciprocal (26 × 29, 31, 33), 85 seeds from 37 capsules, 1 white and 9 very pale green lethals, 62 nonhybrids.

31, 33 × *D. insignis* (14): 104 seeds from 24 capsules, 3 white lethals, 14 nonhybrids; reciprocal, 78 seeds from 17 capsules, 1 yellowish lethal, 40 nonhybrids.

31 × *D. elegans* var. *brachypetala* (39): 38 seeds from 2 capsules, no hybrids, 11 nonhybrids; reciprocal (29 × 39), 12 seeds from 11 capsules, no hybrids, 11 nonhybrids.

CHROMOSOMES: $n = 11$ in population 29 (metaphase I, anaphase II), in population 33 (metaphase I, metaphase II), and in population 47 (diakinesis, metaphase II, anaphase II); meiosis quite regular throughout.

Seeds sown in February germinated readily, and the plants flowered in 45 days in 1951, 48–52 days in 1953. However, seeds sown at Cambridge on Dec. 8, 1949, and cultivated without supplemental light required 80–90 days, with growth proceeding very slowly through the first two months. The first flower bud appeared in the axil of the fifth leaf above the cotyledons. The flowers had a delicate fragrance reminiscent of that of *Syringa vulgaris*.

The hyaline lines on the ovary, which mark the valves of the capsule, are quite conspicuous in the living plant, even being reddish in color in some individuals. The prompt dehiscence of the capsule necessitates special care in harvesting seeds.

The form of the corolla and its lack of purple spots, the capsule splitting at maturity, and the seeds with spiral cellular markings on the seed coat, all features stressed by McVaugh, are characteristic. Although I have seen the species growing only in Tuolumne and Madera counties, California, it was evident there (and from the cultures subsequently grown) that the amount (intensity) and distribution of anthocyanin in the corolla varies greatly both within and between populations. Crosses between populations from this region (29, 31, 33) resulted in good seed-set and green, vigorous seedlings. McVaugh's disposition of *Downingia pallida* Hoover (described from adjoining Stanislaus County) as a synonym of *D. cuspidata* is undoubtedly the correct one.

The interspecific data show the strong genetic barriers characteristic of other species of the genus. However, it is noteworthy that when *Downingia cuspidata* is used as the seed parent in crosses with *D. bicornuta* vars. *bicornuta* and *picta*, *D. ornatissima*, and *D. concolor*, albino seedlings are produced, whereas the reciprocal crosses usually fail even to set seeds. A single count of 1000 pollen grains from a plant of population 31 showed 99.3 per cent stainable grains.

Downingia elegans var. **brachypetala** (Gandoger) McVaugh

FLOWER MORPHOLOGY AND COLOR: See *fig. 3* for conformation of corolla and general color pattern; see also McVaugh (1941, p. 55). Corolla tube broadly funnelform, the lateral sinuses much deeper than the dorsal, the two upper lobes reflexed, often divergent; lower lip concave, about equalling the upper lobes in length, merging gradually with the tube, the three lobes parallel; corolla light blue, the tube pale without, the lower lip with a cen-

tral area of white, lacking ridges or yellow spots in the throat; lower side of corolla tube within pale, with an ill-defined, more or less diffuse bluish-violet spot on either side of the bluish-violet midvein (other veins sometimes bluish violet and visible through the corolla).

COLLECTION GROWN: 39, from the Calapooya River, Linn Co., Oregon, *L. Constance*, 5 Aug. 1950 (seeds).

INTERSPECIFIC CROSSES ATTEMPTED:

39 × *D. concolor* var. *concolor* (34): 34 seeds from 5 capsules, no hybrids, 28 nonhybrids; reciprocal, 99 seeds from 9 capsules, no hybrids, 90 nonhybrids.

39 × *D. ornatissima* (36, 42): 11 seeds from 6 capsules, 1 pale green (probably nonhybrid); reciprocal (with 28, 36), 80 seeds from 16 capsules, no hybrids, 43 nonhybrids.

39 × *D. bicornuta* var. *bicornuta* (30): 24 seeds from 12 capsules, no hybrids, 1 nonhybrid; reciprocal, 8 seeds from 3 capsules, no hybrids, 1 nonhybrid.

39 × *D. bicornuta* var. *picta* (40): not attempted; reciprocal, 13 seeds from 6 capsules, no hybrids, 5 nonhybrids.

39 × *D. cuspidata* (29): 12 seeds from 11 capsules, no hybrids, 11 nonhybrids; reciprocal (with 31), 38 seeds from 2 capsules, no hybrids, 11 nonhybrids.

39 × *D. pulchella* (26): 38 seeds from 9 capsules, no hybrids, 20 nonhybrids; reciprocal, 37 seeds from 10 capsules, no hybrids, 14 nonhybrids.

39 × *D. insignis* (14): 23 seeds from 10 capsules, no hybrids, 11 nonhybrids; reciprocal, 30 seeds from 9 capsules, no hybrids, 11 nonhybrids.

CHROMOSOMES: $n = 10$ (metaphase II) in population 39; meiosis regular.

FIG. 3. Flowers of *Downingia elegans* var. *brachypetala* (top row and bottom row, right) and of *D. insignis* (center row and bottom row, left).

Seeds sown at the end of February, 1951, grew through a relatively long vegetative period. The first buds appeared in the axil of the tenth to fifteenth leaf above the cotyledons in about 45 days, meiosis occurred in about 50 days, and the first flowers opened in about 60 days. Seedlings of this species were easily distinguished from all others grown by the lanceolate, completely entire leaves.

This plant appears to represent *Downingia elegans* var. *brachypetala*, with which it agrees in respect to conformation of corolla and stamens (*fig. 1k*)and habit. It does not have, however, the two yellow spots in the white area on the lower lip which are characteristic of var. *elegans*. The chromosome number ($n = 10$) is distinctive, and, in addition, the plant is completely isolated genetically from the seven other species grown: in no instance was it possible to obtain hybrid seeds in interspecific crosses. In view of these results, McVaugh's suggestion (1941, p. 41) of a hybrid origin for atypical specimens of *Downingia elegans* collected with *D. insignis* (Malheur Co., Oregon, *Cusick 1261* [F]) appears to be an unlikely possibility. The developmental differences between the unilocular ovary with parietal placentation and the bilocular ovary with axile placentation would also seem to be such incompatible ones that hybrids between these species could hardly be expected.

Although this collection of *Downingia elegans* var. *brachypetala* was the only representative which was studied in any detail of the species which are characterized by unilocular ovaries with parietal placentation, it was possible to grow a few plants of *D. yina* var. *major* McVaugh (*D. willamettensis* M. E. Peck), from Corvallis, Benton Co., Oregon, in the spring of 1955. In the latter plants, which began to flower in 68 days, the corolla tube was slender (ca. 5 mm. long), the upper lobes erect, and the anther tube not at an angle to the filament tube. The lower lip was concave, as in *D. elegans* var. *brachypetala*, and the corolla markings were similar, with two light purple dots in the mouth of the corolla tube and no yellow markings on the lip. McVaugh (1941, p. 57) found anomalous collections of var. *brachypetala* which seemed to combine features of *D. yina* var. *major* and suggested that "it is not impossible that var. *brachypetala* is of hybrid origin." Certainly further study of the group composed of *D. montana* Greene, *D. yina* Applegate vars. *yina* and *major*, and *D. elegans* vars. *elegans* and *brachypetala* is in order. Regardless of their interrelationships, however, it is probable that these five taxa with unilocular ovaries comprise a distinctive genetic, as well as morphological, group within the genus.

Downingia insignis Greene

FLOWER MORPHOLOGY AND COLOR: See *figs. 3, 7* for conformation and general color pattern of corolla; note broadly funnelform throat, parallel, ascending upper lobes (with an angle of 20–50° between them), concave lower lip which is not at an angle to the tube; see also McVaugh (1941, p. 40), Mason (1957, p. 749). Corolla sky-blue (to violet-blue, probably sometimes pink or white), the veins darker, the lower lip with a central

white area; white area with two triangular-oblong green or yellow-green spots each extending onto a low fold which ends in a yellow protuberance at the mouth of the corolla tube; green and yellow spots interrupted by a dark violet-purple bandlike spot across each of the folds, the two spots often with diffuse color between or confluent as a band and truncating the central white area; corolla tube within with midveins of the three lower corolla lobes with violet streaks from base to mouth and with 6 or more small reddish-violet spots near the mouth (2 flanking each of the yellow protuberances), a streak of reddish violet extending downward from each spot. See also *figs. 1, 7* (as well as McVaugh, 1941, *fig. 1*; Mason, 1957, *fig. 332c* [*332d* is not characteristic]) for androecium.

COLLECTIONS GROWN:

14, from dry, hard adobe, roadside ditch, ca. 10 mi. s. of Dixon, Solano Co., Calif., *C. E. Wood 7614*, 16 April 1949 (in flower; growing with *Downingia concolor*).

44, on eastern outskirts of Stockton along State Highway 4, San Joaquin Co., Calif., *R. C. Bacigalupi*, 21 April 1951 (seeds).

INTERSPECIFIC CROSSES ATTEMPTED:

14 × *D. concolor* var. *concolor* (15, 20, 34, 87): 131 seeds from 40 capsules, 3 white or very pale green lethals, 45 nonhybrids; reciprocal (with 34, 87), 32 seeds from 21 capsules, no hybrids, 25 nonhybrids.

14 × *D. ornatissima* (27, 35, 36): 75 seeds from 28 capsules, no hybrids, 65 nonhybrids; reciprocal (with 27, 28, 36), 35 seeds from 22 capsules, 2 white lethals, 1 greenish yellow, 26 nonhybrids.

14 × *D. bicornuta* var. *bicornuta* (30): 79 seeds from 13 capsules, no hybrids, 38 nonhybrids; reciprocal, 13 seeds from 4 capsules, no hybrids, 29 nonhybrids.

14 × *D. bicornuta* var. *picta* (40): 18 seeds from 5 capsules, no hybrids, 10 nonhybrids; reciprocal not attempted.

14 × *D. cuspidata* (31, 33): 78 seeds from 17 capsules, 1 yellowish lethal, 40 nonhybrids; reciprocal, 104 seeds from 24 capsules, 3 white lethals, 14 nonhybrids.

14 × *D. pulchella* (25, 26): See below. Abundant seed-set, hybrids very pale green, weak, many inviable, others slow-growing, but if flowering, fertile; F_2 partially lethal, backcrosses to either parent vigorous and fertile.

14 × *D. elegans* var. *brachypetala* (39): 30 seeds from 9 capsules, no hybrids, 11 nonhybrids; reciprocal, 23 seeds from 10 capsules, no hybrids, 11 nonhybrids.

CHROMOSOMES: $n = 11$ (metaphase II) in population 14; meiosis regular.

Seeds planted in February germinated readily, the plants flowering in 51–55 days in 1950, 46–52 days in 1951, and 54–55 days in 1953. Pollen 94.0 to 99.7 per cent stainable. (See TABLE I.)

Although *Downingia insignis* was long confused with *D. elegans*, McVaugh pointed out the numerous differences between the two species and correctly oriented the relationships of *D. insignis* toward *D. pulchella* instead. With *D. laeta* (Greene) Greene (of which I have not seen living

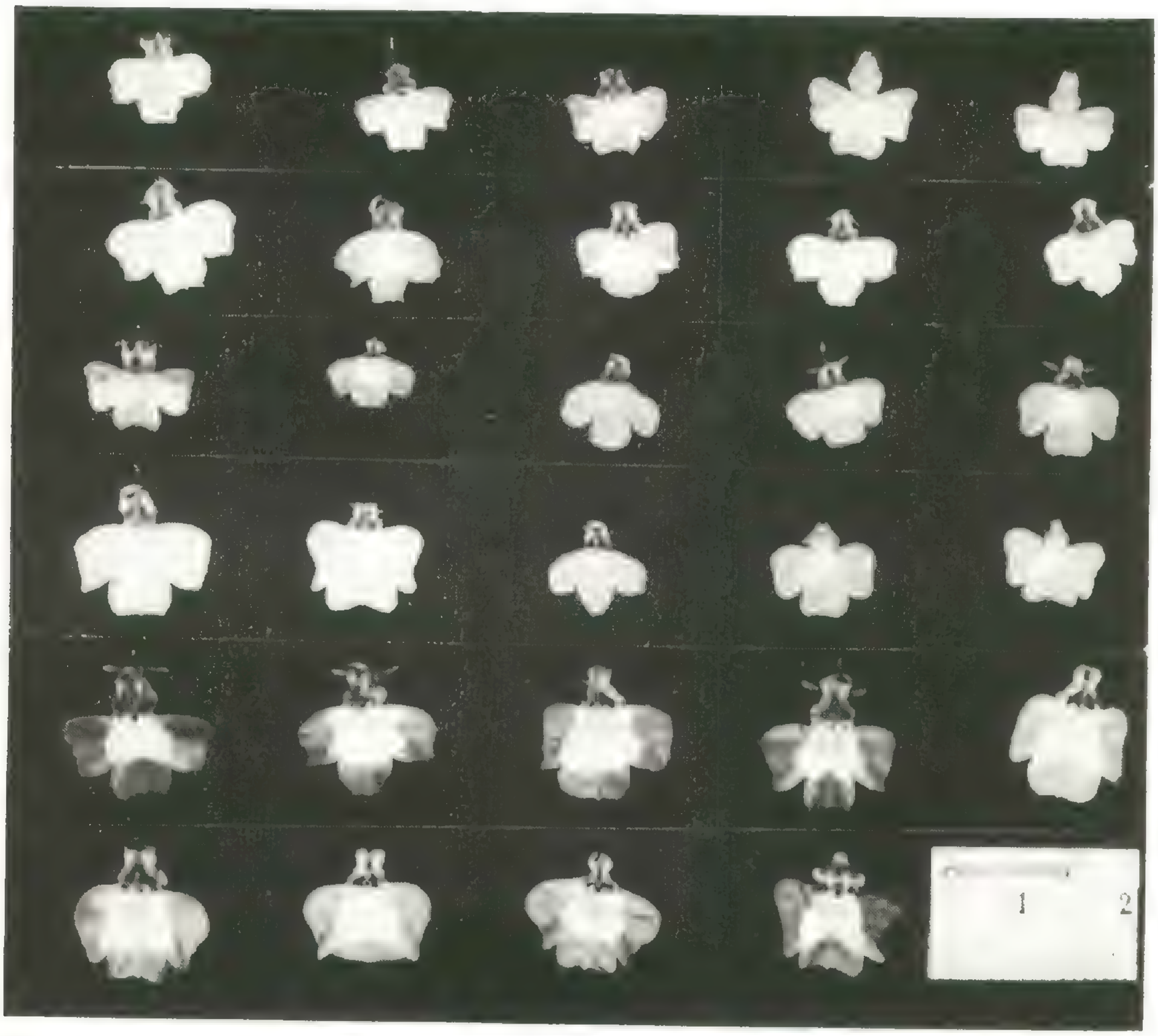


FIG. 4. Flowers of three populations of *Downingia ornatissima* to show geographical variation. Two top rows: Population 35 (var. *ornatissima*), from Tehama County, California. Two center rows: Population 41, from Sacramento County. Two bottom rows: Population 27 (var. *eximia*), from Stanislaus County, California.

material) the two form a group of morphologically related species with strong genetic incompatibilities with other species of the genus, although the chromosome numbers and crossing data show more of a relationship to other species with bilocular ovaries (*D. bicornuta*, *D. concolor*, *D. cuspidata*, *D. ornatissima*, et al.) than to those with unilocular ovaries (*D. elegans* var. *brachypetala*, et al.). The large, concave lower lip not forming an angle with the broadly funnelform corolla tube, the striking color pattern, and the anther tube at right angles to the long filament tube suggest pollination by some fairly large bee.

Downingia ornatissima Greene

FLOWER MORPHOLOGY AND COLOR: See McVaugh (1941, p. 23), Mason (1957, p. 753). Corolla deep blue, violet-blue or violet to pale lilac or nearly white (with only the tips of the lower lobes tinged with blue), with a squarish white central area with two greenish-yellow to bright yellow

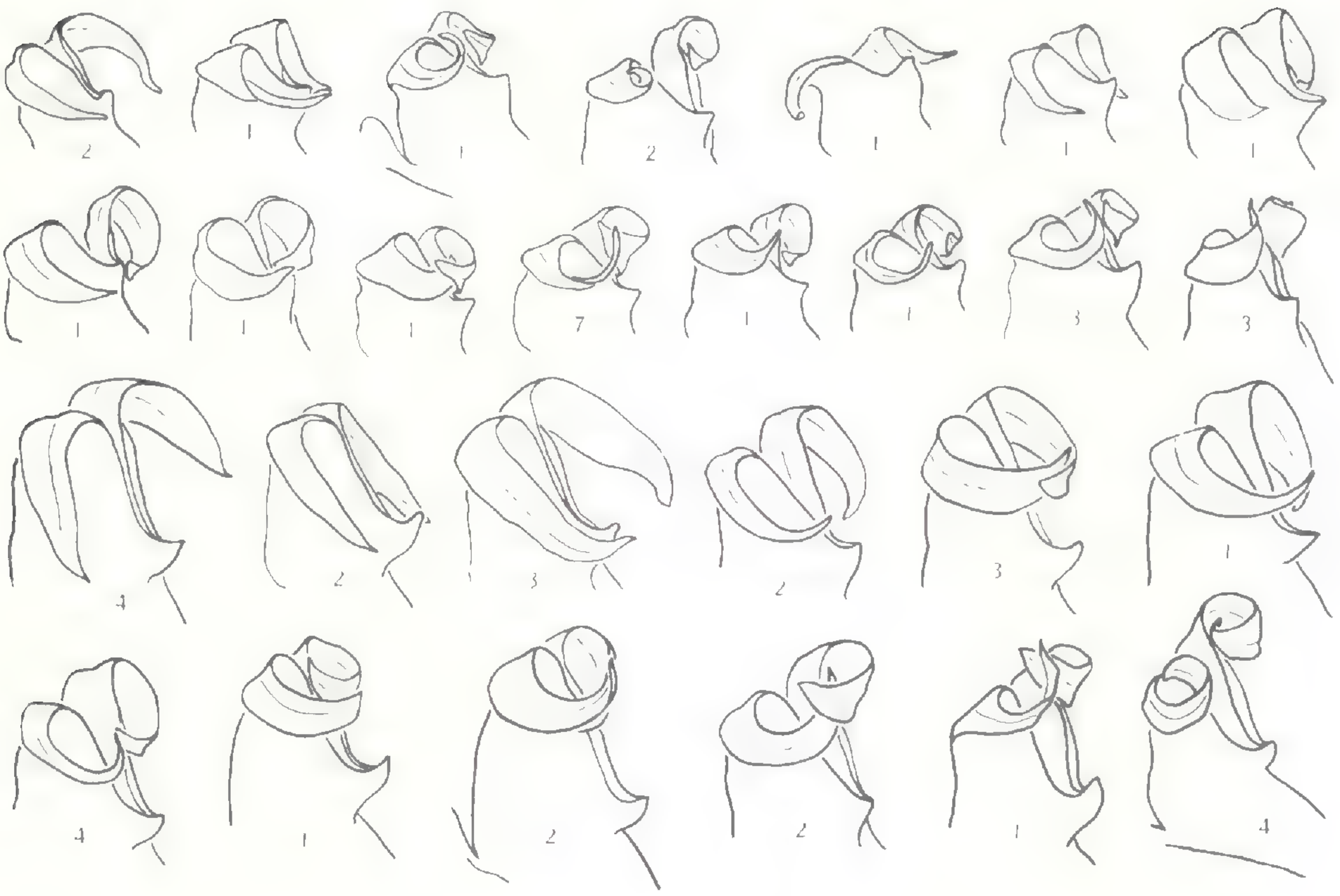


FIG. 5. Upper corolla lobes of two populations of *Downingia ornatissima* to show range of variation in position. Above: Variation in population 36 (var. *ornatissima*), from Tehama County, California. Below: Variation in population 27 (var. *eximia*), from Stanislaus County, California. Hairs omitted from drawings; first four types of first row of population 36 with one or two scattered hairs on each corolla lobe; all members of population 27 with hairs on corolla lobes. Numerals show number of individuals of each type.

spots (sometimes confluent) which extend onto two nipple-like folds at the mouth of the corolla tube; corolla tube with three deep violet to very pale (in pale-flowered forms) spots or streaks alternating with the nipple-like folds, otherwise unmarked; upper lobes and tube concolorous with lower lip but usually paler (white in the palest forms).

COLLECTIONS GROWN:

27, in vernal pool in grassland, ca. 1 mi. sw. of Knight's Ferry, Stanislaus Co., Calif., *C. E. Wood 7627 & C. T. Mason*, 9 May 1949 (only this species present, most plants in fruit).

28, in dry vernal pool on Route 120 at Stanislaus Co. line, Tuolumne Co., Calif., *C. E. Wood 7628 & C. T. Mason*, 9 May 1949 (only this species present; plants in fruit).

35, in dry vernal pool with *Eryngium* in rolling grassland on Route 99W, ca. 8 mi. s. of Corning, Tehama Co., Calif., *C. E. Wood 7635, L. Constance, R. Holm & L. Bonar*, 20 May 1949 (seeds; only this species present).

36, in dry roadside vernal pools with *Eryngium* and *Lythrum* just n. of Corning, Tehama Co., Calif., *C. E. Wood 7636, L. Constance, R. Holm & L. Bonar*, 20 May 1949 (seeds; only this species present).

41, w. of Sloughouse, Sacramento Co., Calif., *G. L. Stebbins, Jr.*, 13 May 1950 (seeds).

42, from low spots in grain field, 3 mi. n. of Sheldon, Sacramento Co., Calif., *G. L. Stebbins, Jr.*, 30 May 1950 (seeds).
45, growing 2 mi. e. of Stockton on State Highway 4, *R. C. Bacigalupi*, San Joaquin Co., Calif., 21 April 1951 (seeds).
48, on Hornitos Road, 2.5 mi. s. of Merced Falls, Merced Co., Calif., *R. C. Bacigalupi*, 22 April 1951 (seeds).

INTERSPECIFIC CROSSES ATTEMPTED:

27, 28, 35, 36 × *D. concolor* (34, 87): 129 seeds from 35 capsules (43 from 1 capsule, 23 from another), 14 white lethals, 52 nonhybrids; reciprocal (34, 87 × 27, 35, 36, 42), 47 seeds from 28 capsules, 1 white lethal, 25 nonhybrids.
27, 28, 36 × *D. bicornuta* var. *bicornuta* (30): 235 seeds from 20 capsules, 15 white lethals, 62 nonhybrids; reciprocal (with 28, 36), 14 seeds from 6 capsules, 2 white lethals, 6 nonhybrids.
27, 28, 36, 42 × *D. bicornuta* var. *picta* (40): 214 seeds from 25 capsules, 7 white lethals, 35 nonhybrids; reciprocal (with 28, 42), 26 seeds from 5 capsules, no hybrids, 10 nonhybrids.
27, 28, 35, 36 × *D. cuspidata* (31, 33): 27 seeds from 41 capsules, no hybrids, 10 nonhybrids; reciprocal (with 27, 35, 36), 536 seeds from 33 capsules, 136 white lethals, 78 nonhybrids (note especially 31 × 27: 293 seeds from 6 capsules, 112 white lethals, 48 nonhybrids).
27, 28, 36 × *D. pulchella* (26): 45 seeds from 23 capsules, 2 white lethals (27 × 26), 30 nonhybrids; reciprocal (with 27, 35, 36), 30 seeds from 18 capsules, no hybrids, 28 nonhybrids.
27, 28, 36 × *D. insignis* (14): 35 seeds from 22 capsules, 2 white lethals, 1 greenish yellow, 26 nonhybrids; reciprocal (with 27, 35, 36), 75 seeds from 28 capsules, no hybrids, 65 nonhybrids.
28, 36 × D. *elegans* var. *brachypetala* (39): 80 seeds from 16 capsules, no hybrids, 43 nonhybrids; reciprocal (with 36, 42), 11 seeds from 6 capsules, 1 nonhybrid.

CHROMOSOMES: $n = 12$ in populations 28 (diakinesis) and 42 (metaphase I, metaphase II), the divisions apparently regular. In population 35 no unequivocal count was obtained, but one slide showed two cells at anaphase I with a chromosomal bridge, in one with an accompanying fragment.

Seeds planted in February germinated promptly; the plants flowered in 54–59 days in 1950, 50–52 days in 1951, 51–55 days in 1953. The first flower bud appeared in the axil of the seventh leaf above the cotyledons. In population 35, two counts of 900 grains showed 99.3 and 99.5 per cent stainable grains, and a count of 1000 grains from a plant of population 28 showed 99.4 per cent stainable grains.

Capsules of this species are very tough and apparently indehiscent. In Tehama County, California, in late May, 1949, the shiny, spindle-shaped seeds were being released and scattered by grasshoppers feasting upon the dry, erect capsules of dead plants which carpeted the bottom of a dried-up vernal pool.

Downingia ornatissima is not to be confused with any other member of the genus. As McVaugh pointed out (1941, p. 26), it is readily recognized

by the small projection at the base of the sinus between the two upper corolla lobes, by the corolla tube sparsely hairy within, by the filament tube which is slightly curved backward and which is longer than the dorsal side of the corolla tube, by the anther tube at an angle to the filament tube, and by the bulbous-tipped hairs on the back of the anthers. It is also unique (for the present, at least) in its chromosome number (12).

The species varies from a plant of the northern part of the Central Valley in which the flowers are pale and small and the upper corolla lobes glabrous within and the tip of each often curled backward into a ring, to one at the south of the range in which the flowers are bright (violet to blue) and larger, and the upper lobes divergent and pubescent within near the tips. (See *figs. 4, 5.*) The two extremes were treated as vars. *ornatissima* and *eximia* by McVaugh, who regarded them as "rather formal varieties, and arbitrarily separated as such." He further realized that "as a result of such arbitrary segregation, a single collection will sometimes contain plants of both varieties" and found "this to be true to the greatest degree in collections from Merced and Stanislaus Counties."

In the three collections of var. *eximia* (27, 28, 48, from Stanislaus, Tuolumne, and Merced counties) studied here, all of the individuals had the upper corolla lobes pubescent, but showed much variation in the divergence or curling of the lobes; the flowers were relatively large and intensely colored (deep blue to violet). Those representing var. *ornatissima* (35, 36, from Tehama County), were paler, smaller-flowered (many with the blue restricted to the tips of the corolla lobes), and in nearly all the upper corolla lobes were glabrous (a few with scattered hairs) and with the lobes curled backward in a ring, although some were merely divergent. Collections from the center of the range (*e.g.*, 41, 42 from Sacramento County) were intermediate in flower-size and -color, with the upper lobes divergent or curled, and glabrous or with a few hairs. In a cross between the northern and southern plants (36 × 28), 335 seeds were obtained from 8 capsules (19–75 per capsule). Only about 130 germinated (perhaps due to the two-year lapse between maturity of seeds and planting), but these were green and vigorous with flowers of intermediate color and size. A clinal situation would appear to be present, but this matter should be pursued, particularly in connection with the possibility of incipient genetic barriers within the species. Taxonomically, however, McVaugh's original conclusion seems to hold, the two geographical varieties being only arbitrarily separable.

Downingia pulchella (Lindley) Torrey

FLOWER MORPHOLOGY AND COLOR: See *figs, 6, 7* for conformation and general color pattern of corolla; note divergent upper lobes (with an angle of 85–120° between them) and the nearly plane lower lip; see also Mc-

Vaugh (1941, p. 37), Mason (1957, p. 750). Corolla bright, deep blue (sometimes violet-blue, pink, or white, the last with all anthocyanin suppressed), the lower lip with a central white area; white area with two roughly triangular or wedge-shaped yellow spots, each covering a low, mound-like fold at the base of the lip (the apex at the mouth of the corolla tube) and with 3 dark-purple spots alternating with the folds; purple spots sometimes confluent across the folds, forming a band and interrupting the yellow area; yellow spots sometimes diffuse, the entire central white area being covered; corolla tube narrowly funnel-shaped, dark reddish purple within (purple without), except for a small white area on the lower side at the mouth. See also below for an exceptional variant.

COLLECTIONS GROWN:

25, from wet, muddy soil, Yolo By-pass, e. of Davis, Yolo Co., Calif., *M. Nobs*, May 1949 (in flower).

26, in heavy, gray, mucky clay around borders of a small pool on Route 50 ca. 2 mi. e. of Dublin, Alameda Co., Calif., *C. E. Wood 7626 & C. T. Mason*, 9 May 1949 (plants very abundant, all in flower).

INTERSPECIFIC CROSSES ATTEMPTED:

25, 26 × *D. concolor* var. *concolor* (15, 34, 87), 86 seeds from 16 capsules, 1 white lethal, 67 nonhybrids; reciprocal (with 15, 20, 34, 87), 27 seeds from 18 capsules, no hybrids, 17 nonhybrids.

26 × *D. ornatissima* (27, 35, 36); 30 seeds from 18 capsules, no hybrids, 28 nonhybrids; reciprocal (with 27, 28, 36), 45 seeds from 23 capsules, 2 white lethals (27 × 26), 30 nonhybrids.

26 × *D. bicornuta* var. *bicornuta* (30): 21 seeds from 10 capsules, no hybrids, 29 nonhybrids; reciprocal, 49 seeds from 5 capsules, no hybrids, 38 nonhybrids.

26 × *D. cuspidata* (29, 31, 33): 85 seeds from 37 capsules, 1 white and 9 very pale green lethals, 62 nonhybrids; reciprocal (with 31, 33), 117 seeds from 20 capsules, 5 white or pale green lethals, 33 nonhybrids.

26 × *D. insignis* (14) and reciprocal: See below. Abundant seed set, hybrids very pale green, weak, slow-growing, many inviable, others flowering and fertile; F_2 partially lethal, backcrosses to either parent vigorous and fertile.

26 × *D. elegans* var. *brachypetala* (39): 37 seeds from 10 capsules, no hybrids, 14 nonhybrids; reciprocal, 38 seeds from 9 capsules, no hybrids, 20 nonhybrids.

CHROMOSOMES: $n = 11$ (metaphase II) in population 26; meiosis regular.

Seeds planted in February developed rapidly, the plants flowering in 46–54 days in 1950, and 46–51 days in 1951. Pollen counts showed 90.9 to 99.6 per cent stainable pollen. (See TABLE I.)

With its showy and distinctive corollas 1.5 cm. across and its characteristically exserted filament tube and tapered anther tube, *Downingia pulchella* is not to be confused with any other member of the genus. On morphological bases, McVaugh thought *D. pulchella* to be most closely related to *D. insignis*, a conclusion which is borne out on the basis of chromosomal and genetic data, the two producing weak but fertile hybrids.

Also of this relationship is *Downingia laeta* (Greene) Greene, which ranges from northeastern California, western and central Nevada, and Utah, north to southern Saskatchewan, Montana, southern British Columbia, and western Oregon, to the north and east of *D. pulchella* and *D. insignis*, both of which are primarily Californian. This small-and-pale-flowered species has an androecium and a general corolla pattern most reminiscent of *D. pulchella* and suggestive of derivation from a similar type.

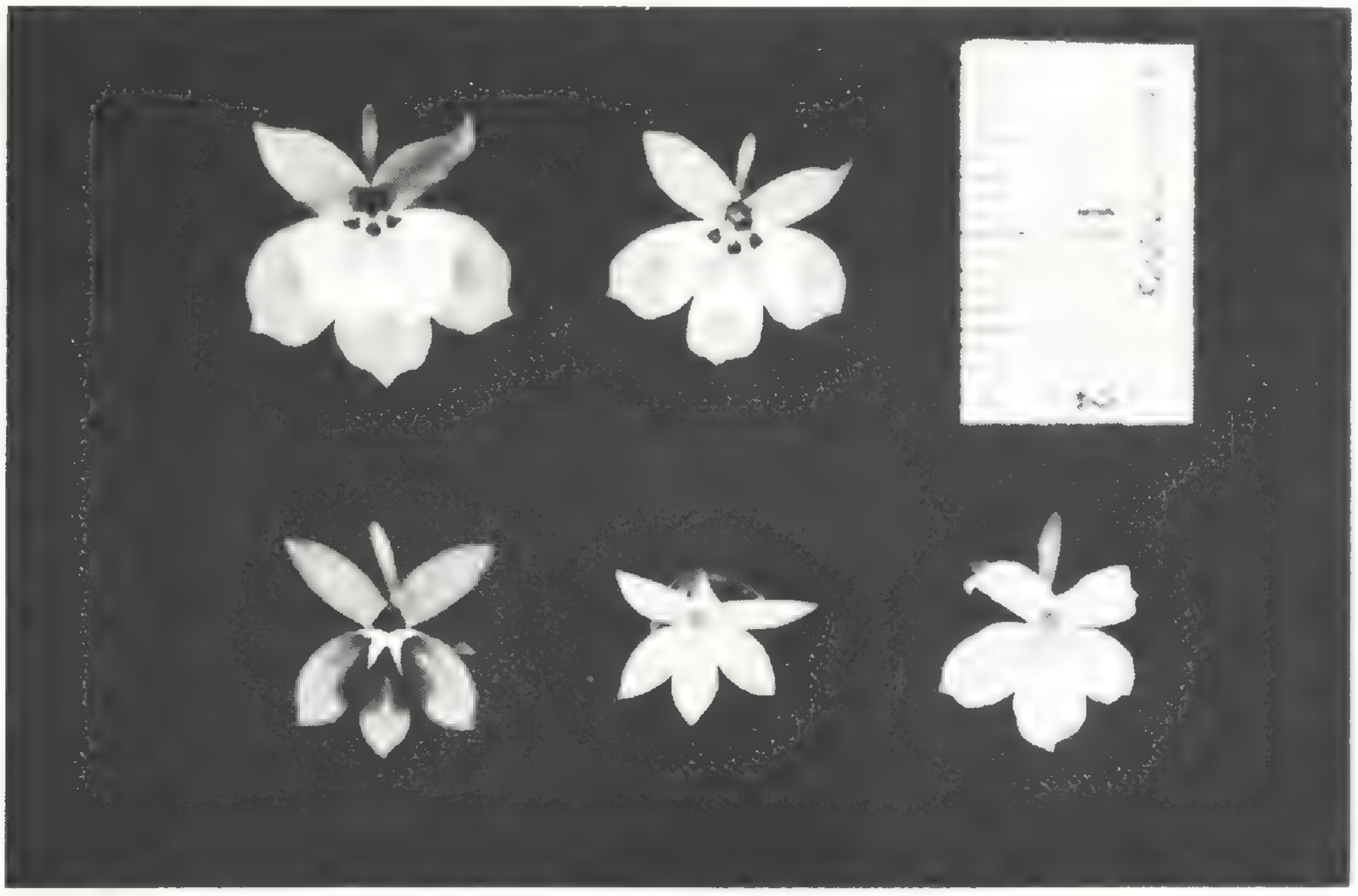


FIG. 6. Variants of *Downingia pulchella*. Upper row: left, the common blue-flowered form referred to in text as "wild type"; right, form with pink corolla lobes. Lower row: left, a small, dark-flowered form; right, form with white flowers, all anthocyanin suppressed; center, a white, small-flowered form from the F_2 of a cross between the two preceding. Flowers seen from above, stamens removed.

An unusual small-flowered mutant form of *Downingia pulchella* which was found in Alameda County, California (see population 26) is of interest in connection with the development of corolla forms and color patterns in the genus. The colony consisted of thousands of densely packed plants, the entire ground appearing to be carpeted with the flowers. Most of the plants bore flowers of the usual blue type described above, but with considerable variation in flower size and in the development of the three spots on the lower lip. Scattered patches of violet, pink, very pale blue, and white plants occurred, with a very few in which the blue anthocyanin was restricted to the tips of the corolla lobes, and at least four in which the white area of the lower lip was strongly suffused with yellow. In addition to these, there were two areas of scattered plants in which the

corollas were small (ca. 1 cm. across) and the lower lip much reduced, all five corolla lobes appearing to be of approximately equal size. (See *fig. 6.*) The corolla was blue, the white central area was completely lacking, a deep violet area extended from the sinuses between the three lobes toward the base of the lip, and the two yellow areas at the mouth of the corolla tube were restricted as shown in the photograph. On the basis of the corolla alone, these plants were so aberrant that one would hardly suspect that they represented *D. pulchella*; yet it was the only species present in this locality and the stamens were the characteristic ones of *D. pulchella*.

A few simple intraspecific crosses were made later with one of these small, dark "mutants" transplanted from the wild. When crossed with a "wild-type" blue-flowered plant (from population 25 to avoid the possibility of heterozygosity), all of the F_1 plants were of the wild type in respect to both color pattern and corolla conformation. An F_2 obtained by selfing one of these plants was composed of 66 of the wild type and 25 of the mutant type. The small, dark mutant crossed onto one of the white-flowered plants from the same colony also produced an F_1 with flowers of the wild type. The F_2 of 84 individuals from a capsule pollinated from the same plant included 47 of the wild type, 17 white, 16 of the small dark mutant, and 4 of a plant with small white flowers (see lower center, *fig. 6*). The expected results from a cross involving two recessive genes would be in the ratio of 47: 16: 16: 5 for a progeny of 84 plants. The two forms thus segregate independently, and the small, dark mutant behaves as though controlled by a single recessive gene which changes both corolla shape and color pattern. As to whether a gene mutation or some larger chromosomal change or rearrangement is represented, I would not guess, especially since the cytology of these plants was not studied.

So different is the corolla size, the form of the lower lip, and the color pattern, however, that the question arises as to whether a "mutation" of this kind (whatever its nature) might not lead to differential selection by the insect pollinators of this group in which the corolla conformation and color pattern and the anther position are so highly specific.

The general conformation of the corolla is suggestive of *Downingia laeta* (see McVaugh, 1941, *figs. 8, 9*; Mason, 1957, *fig. 340*) and, in fact, of *D. pusilla*, the other species with reduced flowers. The color pattern of the former is quite different, but that of the latter is very similar to the pattern of the double recessive obtained above. One is tempted to postulate the derivation of *D. laeta* from a plant similar to *D. pulchella* and of *D. pusilla* from a plant similar to *D. cuspidata* through changes of this kind.

Downingia pusilla (G. Don) Torrey

FLOWER MORPHOLOGY AND COLOR: See McVaugh (1941, p. 35), Mason (1957, p. 761). Sepals 4–5 mm. long. Corolla limb 4–5 mm. across, the lobes divergent from the tube, the upper and lower lips in about the same plane; lower lip much reduced, the lobes 1.5–2 mm. long, the sinuses extending almost to the mouth of the corolla tube; upper corolla lobes parallel or spreading, about equalling the lower; corolla tube narrow, ca. 2 mm. long; corolla white, unmarked except for a yellow spot at the sinus on either side of the lowermost lobe, the two spots confluent across the lobe at the mouth of the tube.

COLLECTION GROWN: 2063, from 5 mi. n. of Snelling, Merced Co., *R. F. Hoover 2063*, 4 May 1937 (GH) (fruit).

INTERSPECIFIC CROSSES ATTEMPTED:

2063 × *D. concolor* var. *concolor* (34): not attempted; reciprocal, 71 seeds from 2 capsules, 48 weak and nearly white lethals, some surviving almost 4 weeks.

2063 × *D. cuspidata* (29, 31): stigmas protruding from anther tube, flowers not emasculated, 61 seeds from 5 capsules, no hybrids, 47 nonhybrids, 2 capsules each with 25 flat and twisted seeds which aborted near maturity; reciprocal (with 31), 39 seeds from 2 capsules, no hybrids, 20 nonhybrids.

CHROMOSOMES: $n = 11$ (metaphase I, $2n = 11$ bivalents). The plants and buds were so small at the time of meiosis that only a single bud in which only one clear cell was countable was found.

The adaptation of this diminutive species to a fleetingly moist habitat is reflected in the longevity of its seeds and the rapidity of its development. Seeds from *Hoover 2063* in the Gray Herbarium germinated readily fourteen years after collection. Flower buds were visible in 21–28 days when the plants were only 1–1.5 cm. high; meiosis occurred in 26–30 days; and the plants began to flower in 39 days in 1951 or 36 days in 1953. At time of flowering the plants were approximately 4 cm. tall, and most of the photosynthetic area of the plant resided in the ovaries and sepals.

Downingia pusilla appears to be self-pollinated, for the most part, all plants in culture setting abundant seeds, in contrast to other species. Some stigmas protrude, but many expand within the anther tube. Although the possibility of pseudogamy has not been ruled out, other types of apomixis appear unlikely, for when the flower was emasculated or the stigma removed completely seeds were not set. Relatively little pollen was produced by these tiny flowers, and it was difficult either to obtain sufficient amounts for hybridization experiments or to remove the anther tube from this species.

The few crosses attempted with other species are inconclusive, but the chromosome number, the corolla, and the spirally marked seeds all seem to corroborate the relationship of *D. pusilla* to *D. cuspidata* postulated by

McVaugh. *Downingia pusilla*, the most reduced species of the genus, represents one of the end points in the evolution of the group, though one attained without change in chromosome number.

Mason (1957, p. 761) has suggested the possibility of two races of this species, noting that plants from north of San Francisco Bay have white flowers and a corolla tube longer than the lobes, while plants of the Central Valley have blue corollas, a tube shorter than the lobes, and the lower lip conspicuously spreading and often with a distinct palate. *Hoover 2063* should belong with the latter group, but it had, however, no trace of blue in the flowers; the tube and corolla lobes appeared to be approximately equal.

DOWNINGIA INSIGNIS × PULCHELLA, A WEAK BUT FERTILE HYBRID

Crosses were made between *Downingia insignis* and *D. pulchella* in 1949 and in 1951. Seed-set ranged from about 30 to 100 per capsule and germination rates from 14 per cent in one of the least successful combinations to about 88 per cent in the most successful.

Seedlings were albino to pale yellowish green. Many died in varying lengths of time, but some grew slowly. Those surviving to the time of initiation of flower buds became more vigorous, the ovaries and sepals being green in all instances, presumably adding substantially to the photosynthetic efficiency of the hybrids. From 82 to 108 or more than 118 days (the longest period for which records were kept) were required from time of planting to time of production of the first flowers.

The various crosses between the two species are summarized below.

Downingia insignis × *pulchella* (F_1):

92 (14 × dark, small-flowered mutant of 26): ca. 125 seeds from 2 capsules, ca. 65–75 pale green hybrid seedlings, about 40 surviving six weeks, one producing a very small and pale flower in 100 days, this and other plants later succumbing to attacks of white flies and mites.

95 (14 × white 26): ca. 50 seeds from 1 capsule, 44 pale green seedlings, 37 surviving at time of first flower (82 days after planting), 20 plants surviving to flower. (See below.)

96 (14 × 25): ca. 90 seeds from 1 capsule, 8 hybrid seedlings all pale and spindly, none surviving more than 40 days.

99 (14 × 25): ca. 80 seeds from 1 capsule, 17 very pale and weak hybrids, none reaching flowering, 1 nonhybrid.

100 (14 × pink 26): ca. 35 seeds from 1 capsule, 7 very pale green hybrids, no survivals.

153 (14 × 26): 50 seeds sown, 38 hybrids, 1 nonhybrid; all hybrids pale green and weak: 3 lasting 65 days, 1 almost reaching flowering (108 days), but succumbing to an attack of *Botrytis*.

157 (14 × 26): 104 seeds (of ca. 335 from 2 capsules) sown, 70 per cent germinated; 64 white or pale green hybrids, 9 nonhybrids; 4 hybrids still alive after 118 days with buds but as yet no flowers.

Downingia pulchella × *insignis* (F_1):

93 (26 white × 14): 75 seeds from 1 capsule; 11 very pale and spindly hybrids, only one surviving to flower; 1 nonhybrid [white-flowered *D. pulchella*].

94 (26 white × 14): ca. 75 seeds from 1 capsule; 22 pale and spindly hybrids, none of which survived more than 50 days, nor flowered; 2 nonhybrids (white-flowered), in 56 days.

98 (25 × 14): ca. 100 seeds from 1 capsule; ca. 25 pale and spindly hybrids, none of which survived to flower; 4 nonhybrids (blue-flowered, one with 3 spots at base of lip confluent in a band).

101 (25 × 14): ca. 200 seeds from 2 capsules; ca. 75 spindly, pale green seedlings, most dead within 50 days (one surviving to flower); 6 nonhybrids (the first flowers in 48 days).

154 (26 × 14): 100 seeds sown; 58 pale hybrids, none surviving more than 63 days, none flowering.

FIG. 7. Flowers of *Downingia pulchella* (above, left, and lower row of five flowers) and of *D. insignis* (above, right, and upper row of five flowers).

FIG. 8. Flowers of first-generation hybrid (population 95) of *Downingia pulchella* and *D. insignis*: a, c, flowers of two plants to show form and color pattern of corolla; b, flower with markings omitted, to show androecium and conformation of upper and lower lips. Compare with *figs. 1m, s* and *7*.

155 (26 × 14): 29 seeds from 1 capsule: 24 pale green hybrids, 6 surviving 70 days, but none surviving to flower (a heavy growth of *Vaucheria* on the soil surface perhaps partly responsible).

156 (25 × 14): 100 seeds planted; 52 pale yellowish-green hybrids; 1 nonhybrid (removed); 5 hybrids (all pale and spindly) surviving to flower after 103 days.

Population 95, a cross between the blue-flowered *Downingia insignis* and a white-flowered plant of *D. pulchella*, was the most successful of the hybrids. In this population, sown 17 February 1950, germination was 88 per cent, proceeding over a three-week period. The seedlings were all pale yellowish green and very slender and grew slowly, the largest being only 1.3 cm. tall after seven weeks. When the first flowers opened, 82 days after sowing, 37 plants from 0.4 to 14 cm. tall still survived. Twenty plants lived to flower by May 20. The stems of all of these remained very pale green, reddish near the base. The leaves produced up to the time of flower-bud initiation were pale, but those with axillary flower buds were bright green, and the ovaries of all flowers were green.

The two parental species differ in a whole series of floral characteristics, many of which will be immediately apparent from an inspection of *fig. 7*. Among those of the corolla are the shape, length, and diameter of the tube; the form and concavity of the lower lip and its angle to the corolla tube; the angle between the upper lobes and their angle to the tube; and the markings of the lower lip and the corolla tube. Features of the androecium include the length of the filament tube; the length, shape, and color of the anther tube and its angle to the filament tube; and the length and shape of the hairs on the anther tube.

The flowers of the F_1 hybrids were intermediate in most respects (see *fig. 8*), in shape more suggestive of *Downingia insignis* but with a much

narrower corolla throat, a somewhat flatter lower lip and more divergent upper lobes. The color pattern was also intermediate: the white area had the general form of that of *D. pulchella*, but showed the restriction evident in *D. insignis*, and the three dark spots at the base of the lip varied from separate, but larger than usual in *D. pulchella*, to more or less confluent in a narrow band across the two low yellow folds, undoubtedly reflecting the heterozygosity of the parental plants. (Self-pollination of wild plants of *D. pulchella* produces offspring with considerable variation in the shape of the corolla and in the spotting of the lip, sometimes with much larger spots and these sometimes confluent across the low ridges as above.) The

TABLE I. Pollen Fertility in Downingia insignis, D. pulchella, and Hybrids

POPULATION	TOTAL GRAINS COUNTED	PER CENT STAINABLE POLLEN	PER CENT ABORTED POLLEN
D. insignis			
14	1600	94.0	6.0
14	2100	99.4	0.6
14	1800	98.9	1.1
14	1500	98.3	1.7
14	1800	99.4	0.6
14	2000	99.7	0.3
D. pulchella			
26	2000	99.6	0.4
26, white, selfed	1200	90.9	9.1
25	1600	98.0	2.0
25	1600	98.1	1.9
D. insignis × *pulchella* (F_1)			
95	1100	94.2	5.8
95	1500	93.7	6.3
95	1800	98.8	1.2
95	850	94.6	5.4
D. pulchella × *insignis* (F_1)			
93	975	95.2	4.8
93	930	92.9	7.1
101	1350	95.8	4.2 [a]
D. insignis × *pulchella* (F_2)			
203 (95 × 95)	1000	98.7	1.3
203	1100	95.4	4.6 [b]
203	1200	90.8	9.2 [c]
203	1000	97.2	2.8 [d]
203	1100	99.1	0.9

[a] Including three giant grains, and many grains slightly smaller than usual; greater variation in pollen size than usual.

[b] Considerable variation in size; pollen grains appearing much below normal counted as aborted although contents present.

[c] No size variation; all grains clearly aborted.

[d] Considerable variation in size, including grains larger and smaller than normal.

androecium is also intermediate: the filament tube in length and the anther tube in shape, angle to the filament tube, and marking (slightly darker than the dirty white anthers of *D. insignis* but lighter and less pronouncedly blue-gray striped than in *D. pulchella*). The hairs on the anther tube were slender and intermediate between the short, stubby hairs of *D. insignis* and the relatively long, slender ones of *D. pulchella*. Aside from the variation in the dark spots at the base of the lower lip, the flowers of the twenty plants of this population were remarkably uniform. Although the flowers generally were somewhat smaller in size than those of either parent, this, as in many annuals, was related to the vigor of the plant rather than to other factors, the most vigorous of the hybrids also bearing the largest flowers. The ovaries ranged from 2.5 to 3 cm. in length and the capsules from 2.5 to 3.7 cm.

Chromosome counts were not attempted on the hybrids because of the small number of surviving plants and their general lack of vigor. Pollen counts, however, showed a range of pollen stainability (and presumably fertility) of 92.9 to 98.8 per cent, approximately the same as that of the parental species. (See TABLE I.) Seed set by the hybrids and in backcrosses bore out this supposition of fertility. However, the pollen variations seen in the surviving plant of population 101 suggest at least a low frequency of meiotic irregularities.

Backcrosses. A number of backcrosses from populations 93 (a single surviving plant) and 95 were made to each of the parents. The hybrid was used as the pollen parent in all except a single instance because of the general weakness of the hybrid plants and the desirability of using the relatively few flowers for the production of a second hybrid generation. The results are summarized below:

BACKCROSSES OF F_1 TO *Downingia pulchella*:

205 (26 white × 95): 85 seeds from one capsule, 77 green seedlings, 1 albino lethal; all greens vigorous, the first flowers in 52 days.

206 (95 × 26 white): ca. 75 brown seeds plus an approximately equal number of nearly white seeds from 1 capsule; ca. 95 germinated, ca. 63 white or pale lethals, 22 pale and weaker, 10 vigorous and green which flowered after 52 days. (Possible contamination with F_1 pollen? Cf. F_2 below.)

207 (26 × 95): 260 seeds from 3 capsules, 1 albino lethal, 210 green and vigorous, the first flowers in 47 days.

208 (26 × 95): 70 seeds from 1 capsule, 65 green and vigorous seedlings, the first flowers in 45 days.

209 (26 × 95): 100 seeds from 1 capsule, good germination (number not recorded), all seedlings green and vigorous, the first flowers in 45 days.

210 (25 × 93): 100 seeds from 1 capsule, 1 white lethal, numerous green and vigorous seedlings (not counted), the first flowers in 47 days.

BACKCROSSES OF F_1 TO *D. insignis*:

211 (14 × 93): 157 seeds from 2 capsules, 1 white lethal, numerous green and vigorous seedlings (not counted), first flowers in 47 days.

212 (14 × 95): 649 seeds from 9 capsules (ca. ½ sown), 1 pale lethal, numerous green and vigorous seedlings (not counted), the first flowers in 47 days.

213 (14 × 95): ca. 120 seeds from 1 capsule, numerous green and vigorous seedlings, the first flowers in 50 days.

With the exception of the possibly contaminated cross (206) in which the hybrid was used as the seed parent, in each of the combinations above the seed-set and excellent germination indicate full fertility and vigor. The seedlings were green and vigorous, grew rapidly, and flowered in 47–52 days, the period required for the parental species. As would be expected, the variation ranged roughly from the F_1 to the backcross parent. Populations obtained from backcrosses in each direction are shown in *figs. 9* and *10*.

Only one plant of population 209 was examined cytologically. Numerous divisions at anaphase I and metaphase II were seen. All divisions appeared to be regular, except for two cells at anaphase I showing traces of a lagging chromosome or bridge and one at metaphase II with one plate of eleven chromosomes, the other of eleven plus a fragment.

The Second Generation. Various combinations of the single survivor in population 93 (*Downingia pulchella* × *insignis*) and those in 95 (*D. insignis* × *pulchella*) were tried in 1950. The results are summarized below:

Downingia insignis × *pulchella* (F_2):

200 (93 selfed): 181 seeds from 3 capsules from a single plant, 59 white or pale green lethals, 117 varying from weak and pale, to vigorous and green, most plants green eventually but some definitely more vigorous than others; first flowers in 52 days.

201 (93 × 95): 142 seeds from 2 capsules (with 12 and 130 seeds), 110 seeds germinating, 55 white or very pale lethals, 55 pale green, yellowish-green, or green seedlings showing great variation in vigor, 0.9–6.5 cm. tall after 42 days; first flowers in 50 days.

202 (95 × 93): 2 seeds from each of 2 capsules, 1 white lethal, 1 pale green (died in 30 days), 2 slow-growing pale greens flowering after 60 days.

203 (95 × 95): 454 seeds from 8 capsules, 114 white or pale green lethals, 85 yellowish-green to green survivors with much variation in vigor (0.5–4.4 cm. tall after 42 days), first flowers after 52 days.

204 (95 selfed): 68 seeds from one capsule, 31 white or pale lethals, 23 of various shades of green surviving, with wide range of vigor (0.6 to 1.8 cm. tall after 42 days), no record of flowering.

Seed set averaged 50 to 70 (extremes 2–130) per capsule and germination was generally excellent. Thirty to fifty per cent of the F_2 seedlings were albino or pale green lethals, while the remainder ranged from pale green to vigorous, bright green plants, many of which survived to maturity. In contrast to the F_1 generation, flowering began in about 52 days (approximately the same period required for the flowering of the parents). Pollen stainability (see TABLE I) ranged from 91 to 99 per cent in five plants of population 203.

Obviously many segregant combinations were eliminated in the F_2. As

FIG. 9. Flowers of thirty plants of a backcross, population 211: *Downingia insignis* (14) × (*D. pulchella* × *insignis*, population 93). Natural size.

will be seen from *figs. 11* and *12* which illustrate individuals of populations 200 and 203, the recombinations in no instance duplicate the parental types exactly, and most resemble the F_1. Although the *Downingia pulchella* parent in the original crosses was white-flowered, the few white-flowered

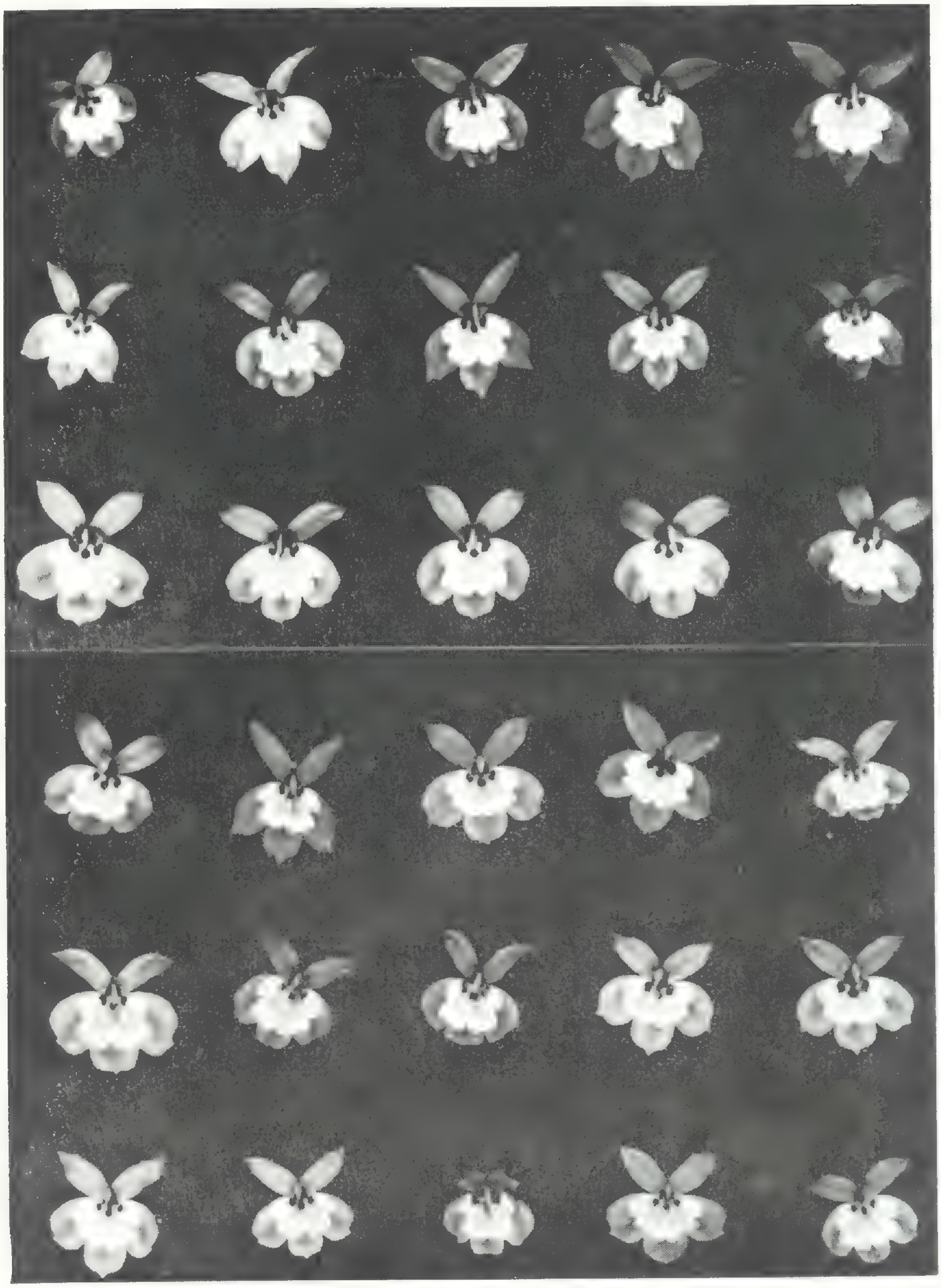


FIG. 10. Flowers of thirty plants of a backcross, population 207: *Downingia pulchella* (26) × (*D. insignis* × *pulchella*, population 95). Natural size.

segregants in the F_2 were more like *D. insignis*, although with divergent corolla lobes. In one bizarre individual of this population the corolla and androecium were suppressed altogether, but the stigma was well developed, and apparent stigmatic surfaces were found on the tip of each of the sepals.

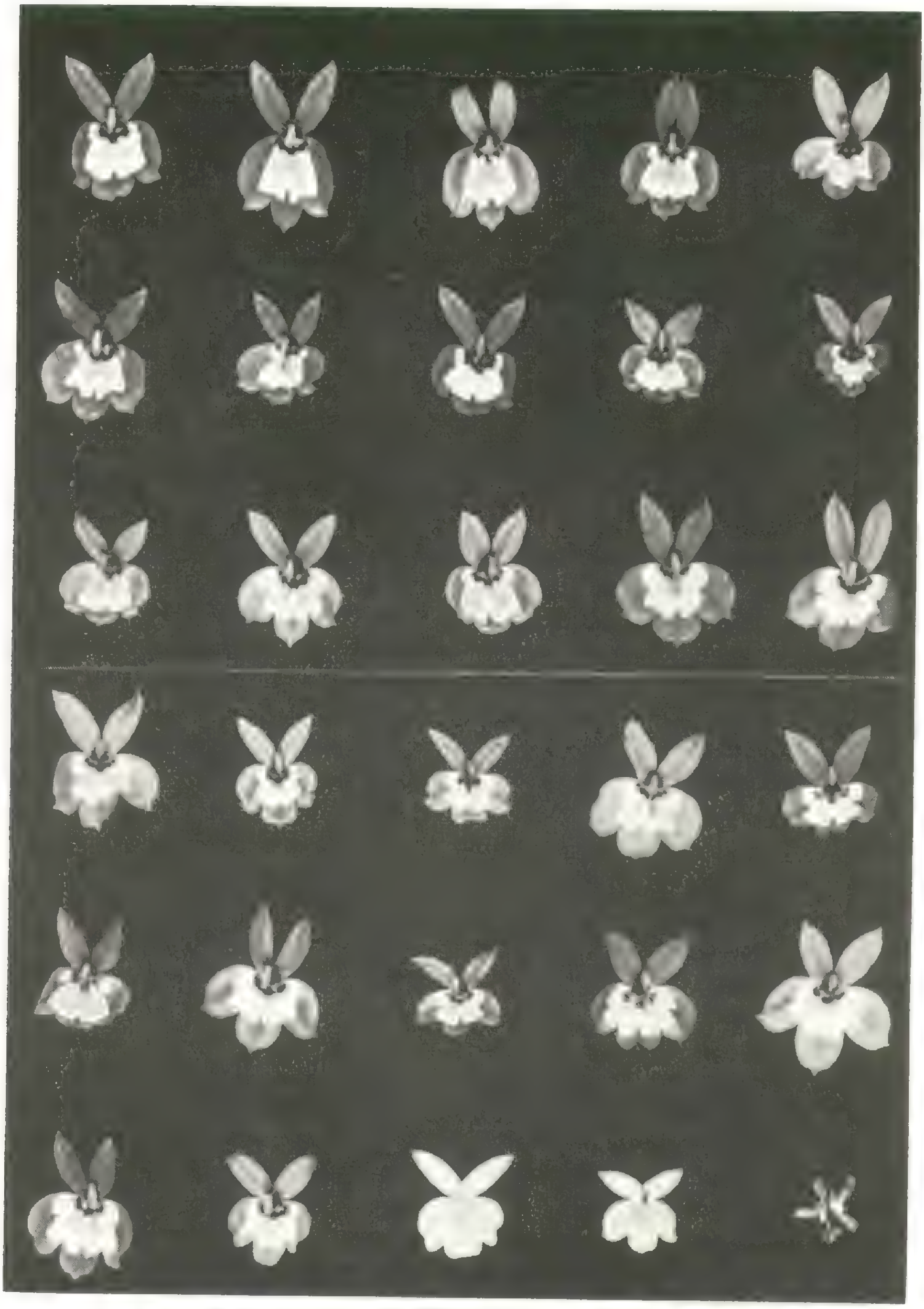


FIG. 11. Flowers of thirty plants of second-generation hybrid of *Downingia pulchella* × *insignis*: population 200 from self-pollination of the single survivor of F_1 population 93. Plant at right in bottom row lacked corolla and stamens and had apparent stigmatic lobes on tips of sepals. Natural size.

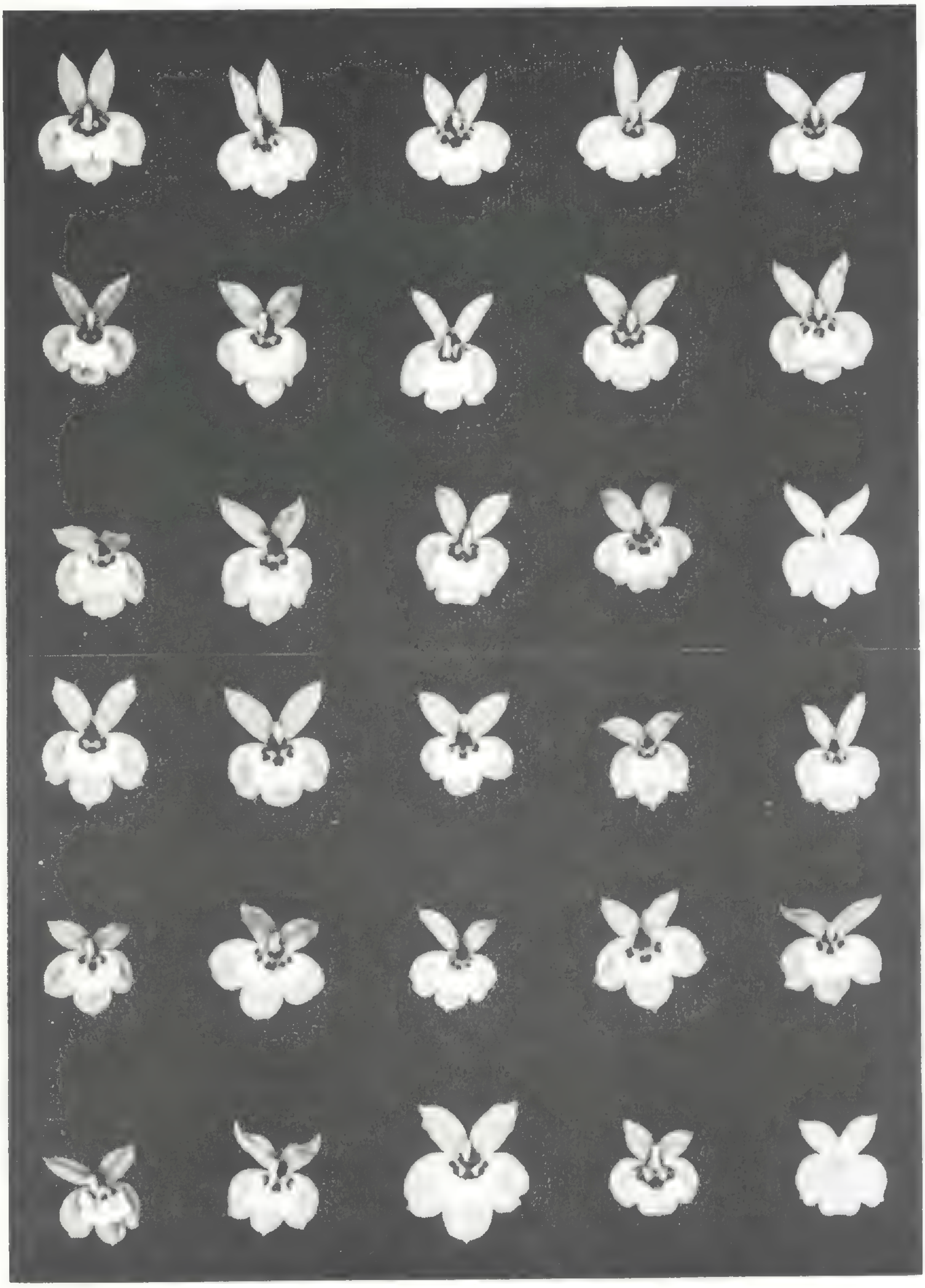


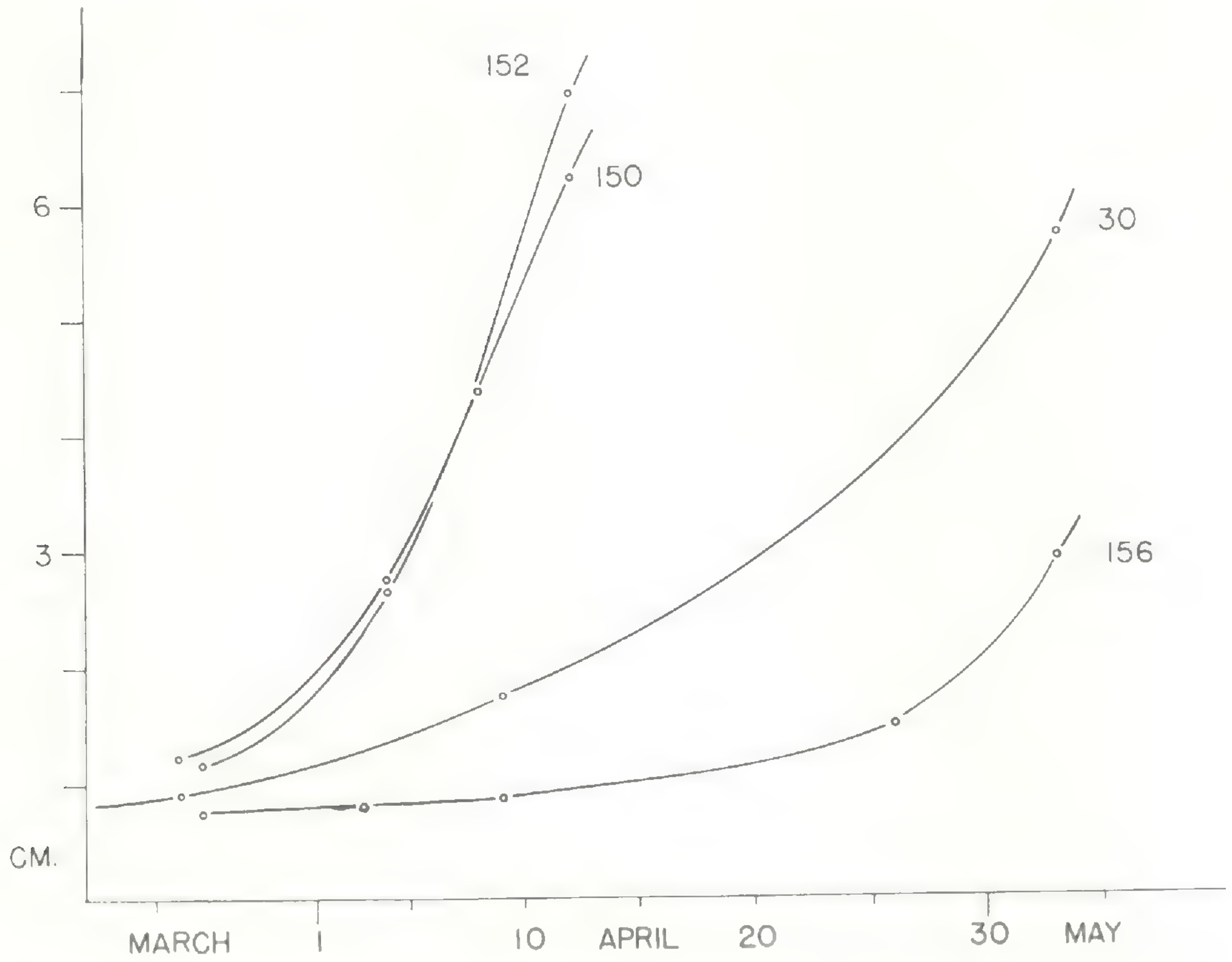
FIG. 12. Flowers of thirty plants of second-generation hybrid of *Downingia insignis* × *pulchella*: population 203 from 95 × 95. The *D. pulchella* parent in this and in *fig. 11* was a white-flowered form. Natural size.

The Third Generation. Most of an F_3 generation was lost at Chapel Hill in 1952, a year in which all seeds sown failed. In 1953, four sowings, each derived from a single capsule and involving a cross within population 200, the F_2 of 93 (*D. pulchella* × *insignis*), were made. Seeds ranged from sixteen to sixty per capsule, but only two to fifteen per capsule germinated, perhaps in part because of the two-year delay in planting. Seedlings were yellow to moderately green, but none was very vigorous. All grew very slowly, and none survived to flower.

From the above data it is evident that hybrids between *Downingia insignis* and *D. pulchella*, both of which have 11 pairs of chromosomes, are easily produced artificially and that germination of hybrid seeds is good. The interaction of the two gene complements produces physiological difficulties, however, and the hybrids are albino or chlorotic, inviable or weak, requiring (when surviving at all) very much longer than the parental species to flower. They are fertile, however, setting abundant seed with other hybrids or producing green and vigorous offspring in backcrosses. The second generation includes many genetically unbalanced plants, including a high proportion of albinos and chlorotic plants which do not survive. However, some of this generation are more vigorous than the first and flower in about the same length of time as the parental species. Although the data on a third generation are quite inconclusive, physiological weakness seems to continue.

In spite of the weakness of the first generation hybrid, there is the potentiality for gene exchange between the parental species, especially by backcrossing. It seems very unlikely, though, that such ever occurs in the wild populations in which *Downingia insignis* and *D. pulchella* grow together (as they sometimes do). No field data are available, but several factors which may work against any genetic exchange are immediately apparent. Insect pollinators of the two species have not, to my knowledge, been studied. The highly specialized flowers suggest, however, the possibility of a barrier to interspecific pollination due to differences in pollinators of the two species, or to differences in the preferences of a single pollinator for a particular color pattern, or to the mechanical barrier of the position of anthers and stigma. Assuming, though, that pollination may occur, the genetic chlorosis of the hybrids and the consequent (?) weakness and slowness of growth would result in the elimination of hybrid plants from wild populations before they could backcross with either parent or mature seeds themselves. The hybrids are either (1) too weak to survive the rigors of the mild winter or of the vernal pool habitat in general, or (2) cannot compete with the parental or other species, or (3) grow so slowly that they are out of synchronization with the drying up of the vernal pools and the flowering of the parental species and may not even be able to flower at all. Any or all are likely.

In the spring of 1951, a number of greenhouse experiments were essayed to test the survival potentialities of hybrids in competition with the parental species. As controls, fifty seeds of each of the parental populations (*D. pulchella* 26, *D. insignis* 14) and of three hybrid crosses (154,



Partial growth-curves of *Downingia insignis* (150), *D. pulchella* (152), their F₁ hybrid (population 156), and the slowest growing of the species, *D. bicornuta* var. *bicornuta* (30). Based on means of heights of varying numbers of plants, graph is intended only to give approximate comparisons of vigor and rapidity of maturation, not statistically accurate growth rates and ranges of variability. Measurements for 150 and 152 were taken respectively from 20 to 36 plants; those for hybrid began with 47 plants but drop to 41, 37, 11, and finally 5 survivors; for *D. bicornuta* involve only two plants grown separately. All seeds sown 28 February 1951; flowering of 150 and 152 began on 12–14 April, of hybrid on 5 June, and of *D. bicornuta* on 6 May.

155, 156; see F_1 above) were planted in 6-inch azalea pots. Ten combinations of hybrid and parental seeds totalling 60 to 300 seeds to each 6-inch pot and in proportions of hybrids to equal numbers of parental seeds of 1:2 to 5:1 were also sown at the same time. Even when grown alone in the controls (see F_1 above), these particular hybrids were hardly successful, and progressed slowly, only five of population 156 surviving to flower after 103 days. In none of the competitions did any hybrids survive to flower, whereas, no matter how crowded the pot, many of the nonhybrids flowered in 45–50 days. Unless combinations of *D. insignis* and *D. pulchella* other than the few tried here produce very much more vigorous hybrids, it seems that a seedling hybrid of these two species stands little chance of survival in the wild.

DISCUSSION

The species of *Downingia* form an aneuploid series with 8, 9, 10, 11, and 12 pairs of chromosomes. Eleven (which occurs in five species) appears

to be the basic number, especially since the less specialized *Porterella carnulosa*, the closest relative of the genus, also has eleven pairs (Carlquist, Madroño 13: 206. 1956).* In addition, both *D. elegans* var. *brachypetala* (10 pairs) and *D. ornatissima* (12 pairs) show morphological specializations indicative of derivation; and the occurrence of eight or nine pairs in different populations of *D. concolor* suggests both specialization and continuation of the aneuploid trend. Hybrids between the two chromosomal races of *D. concolor* should yield evidence from their meiotic behavior of the manner in which aneuploidy has occurred in the genus, and somatic chromosome morphology should provide additional clues.

Chromosome numbers and hybridization data are summarized in *fig. 13*, in which the species have been arranged on the basis of morphological and genetical similarities. The diagram includes reciprocal interspecific crosses in all possible combinations, except some involving *Downingia pusilla* and those between *D. bicornuta* var. *picta* and *D. insignis* and *D. pulchella*, none of which was made.

It is clear from the crossing results that species of *Downingia*, at least as represented by these populations, are well separated genetically, with strong barriers to hybridization. Interspecific crosses fail to produce embryos; the seeds abort near maturity or the hybrid seedlings are albino; or, exceptionally, the hybrids are weak and slow growing but fertile. These categories mark three genetic groups into which the eight species fall.

The first comprises only *Downingia elegans* var. *brachypetala* which stands in complete isolation, for not even partially developed seeds were obtained in any of the hybrid combinations attempted.

A second group, including *Downingia bicornuta*, *D. concolor*, *D. cuspidata*, *D. ornatissima*, and *D. pusilla*, shows very strong interspecific genetic incompatibilities, but the production of more or less numerous albino seedlings in various combinations of these species provides evidence of closer relationships within the group than outside it. The differences found in most reciprocal crosses between these species (e.g., the production of relatively numerous albino seedlings when *D. cuspidata* is used as the seed parent, but the failure to set seeds when this species is the pollen parent) suggest a prefertilization barrier to hybridization, in addition to the strong incompatibilities of the gene complements in the hybrids.

The third includes *Downingia pulchella* and *D. insignis* which are isolated from the other species grown, producing only an occasional albino seedling with some members of the preceding group. The two species are potentially capable of interbreeding, but their hybrids are albino or chlorotic, weak and slow growing. Those surviving to flower, however, are

* McVaugh's earlier report (1943, p. 25) of $n = 12$ for this species (*McVaugh 6282*, Lake County, Oregon) was overlooked when the manuscript was being prepared. Carlquist's count was based on *Mason 14439* (UC), from Sierra County, California. In spite of the apparent aneuploidy in this widespread species ("northwestern Wyoming to southeastern Oregon, south in the mountains to northern Utah, Coconino County, Arizona, northern Nevada, and Tulare County, California"), eleven would still seem to be the basic number in *Downingia*.

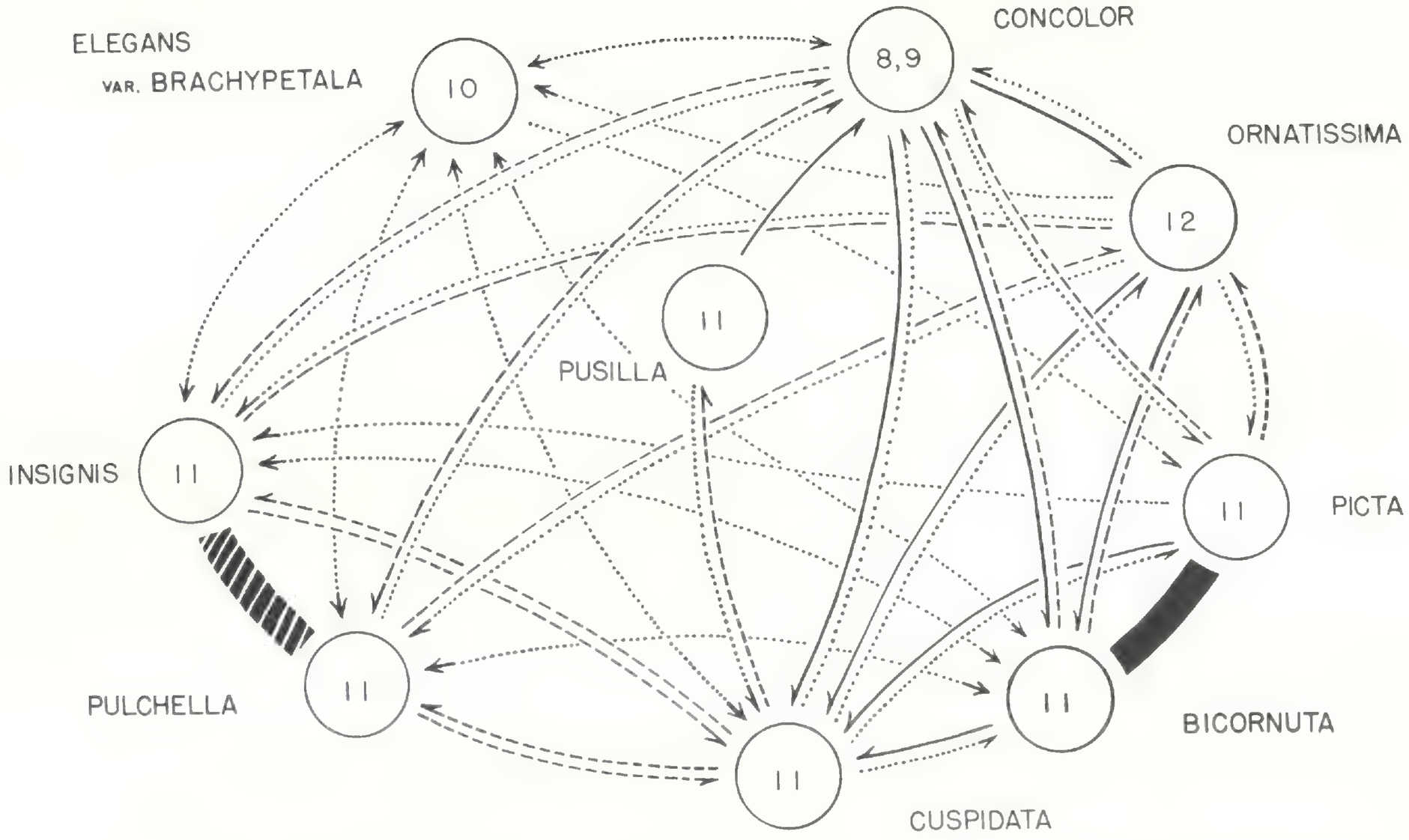


FIG. 13. Crossing relationships and chromosome numbers of eight species of *Downingia*. All crosses attempted are shown. Arrows indicate direction of cross; those unsuccessful in both directions are shown by a single dotted line with arrow at both ends. Dotted line, no trace of hybrid seeds; dashes, production of an occasional albino lethal (averaging less than one per capsule); thin solid line, frequent hybrid lethals; broad striped band, albino or chlorotic but fertile hybrids; broad black band, vigorous fertile hybrids. See text.

as fertile as either parent and produce green and vigorous offspring when backcrossed to the parents. Although they sometimes grow together, the weakness of the first-generation hybrid probably precludes any possibility of gene exchange in the wild, even if hybrid seeds are produced.

In contrast to interspecific crosses, those within species (although limited in number) produced vigorous seedlings. The two recognized varieties of *Downingia bicornuta* (vars. *bicornuta* and *picta*), strikingly different in morphology, geography, and physiology, yield a vigorous and apparently fertile hybrid of intermediate morphology, confirming the taxonomic status accorded them. It is to be expected, however, that further studies will show, in addition to the aneuploidy found in *D. concolor*, other stages in speciation, such as the development of genetic barriers to interbreeding.

Data are lacking for four species, but the chromosome numbers and the genetic results corroborate both McVaugh's taxonomic treatment of the eight species grown and his arrangement of these in three informal morphological groups (which correspond to the genetic categories above). (See McVaugh, 1941, p. 10.) *Downingia bella*, *D. bicornuta*, *D. concolor*, *D. cuspidata*, *D. ornatissima*, and *D. pusilla*, all with bilocular ovaries, form a morphologically and genetically interrelated group of species, while *D. pulchella*, *D. insignis*, and *D. laeta* form another. *Downingia yina* (including *D. willamettensis*) and *D. montana*, with unilocular ovaries, were treated by McVaugh as still another line, while *D. elegans*, also unilocular, was placed in an isolated position, even though the question of hybridization between this species and *D. yina* was raised. *Downingia elegans* var. *brachypetala* is indeed isolated genetically, morphologically, and chromosomally from the other species grown, but it is in many ways similar to *D. yina* var. *major* (*D. willamettensis*), and it is possible that these three species with unilocular ovaries may be more closely related than appeared at first.

Although strong genetic barriers to hybridization now exist, and, in the absence of these, differences in chromosome number might produce at least partial barriers to interbreeding of the species, a number of other barriers may have been important in the past and may be at least partially operative at the subspecific level now. Geographical, ecological, temporal, and mechanical barriers are possible. (See Stebbins, 1950.)

Occurring in both California and Chile, *Downingia pusilla* is the most spectacular example of spatial division of a species; but *D. concolor* var. *concolor*, of Lake to Monterey counties, California, is separated from var. *brevior*, of San Diego County, and *D. cuspidata* seems to be divided into several disjunct areas. *Downingia montana*, of the Sierra Nevada, is separated ecogeographically from its closest relative, *D. yina*, and the same is true of *D. pulchella* and *D. laeta*.

Both ecogeographical isolation and differences in flowering time may play a part in the separation of *D. bicornuta* vars. *bicornuta* and *picta*, which in cultivation flower about two weeks apart. However, subspecific variation in this species is more complex than has been thought and needs further study. *Downingia insignis* and *D. elegans*, perfectly distinct but

long confused taxonomically, also show differences in time of flowering.

Field studies will be necessary to determine whether real ecological differences exist between otherwise sympatric species. Some species do occur together, such combinations as *D. concolor–D. insignis*, *D. elegans–D. insignis*, *D. bicornuta–D. cuspidata–D. concolor*, and *D. pulchella–D. insignis* having been found. Eight species are reported from Stanislaus County, California, but no further information is available as to their distribution within this center of concentration.

Mechanical barriers to crossing are among the most intriguing possibilities. The variation in length and position of the stamens, their peculiar pollen discharge mechanism, and the wide range in size and coloring of the elaborate corollas strongly suggest specific insect pollinators. It does not seem likely, for example, that the same bee which has its face dusted with pollen from the short, included stamens of the modest flowers of *D. concolor* could pollinate nearby *D. insignis* with its large and showy lower lip, broad corolla tube, and strongly exserted stamens. Careful field observations are needed on pollinators and their behavior, not only in respect to the species, but to mutations in the form and color of the corolla. (See *Downingia pulchella* above.)

These eight species of *Downingia* emerge, then, as distinctive, highly specialized semiaquatic winter annuals, well adapted to a transient habitat. A large number of individuals may occur within a small area, but because of the nature of the habitat the populations are discontinuous. Although self-compatible, the plants are adapted for insect pollination and are outcrossing (with the apparent exception of the most reduced species). As a result, individuals are highly heterozygous. The chromosome numbers form an aneuploid series centering around 11, with 8, 9, 10, and 12 as derived numbers. The presence of occasional chromosomal bridges in meiotic divisions and of different chromosome numbers within a single species show that chromosomal repatterning continues within the genus. Poorly to highly differentiated geographical races attest to a whole series of subspecific levels of development. However, the species are well separated, both morphologically and genetically. Although spatial, ecological, temporal, and mechanical barriers may be operative below the specific level, strong genetic barriers exist between species, which, although presumably evolved allopatrically, can now exist sympatrically without gene exchange.

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STUDIES IN THE THEACEAE, XXXII
A REVIEW OF THE GENUS TERNSTROEMIA IN THE PHILIPPINE ISLANDS

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IN THE PHILIPPINE ISLANDS, the genus *Ternstroemia* was first recognized as such when Fernandez-Villar (Noviss. Append. Fl. Philipp. 19. 1880) transferred *Llanosia toquian* Blanco to the genus. Oddly enough, this earliest Latin description of the oldest species in the island group is the best and most completely understandable of all those presented to date.

No species were added to the group until 1912, when Elmer described *Ternstroemia gitingensis*. All of the remaining recognized taxa were described by 1918. All told, there have not been more than ten taxa described or suggested for the genus in this area. In fact, except for *Ternstroemia toquian*, all of the species presented were described by either A. D. E. Elmer or E. D. Merrill.

Most of the species were described from fruiting material and it is from this material that the species are most easily recognized. However, the genus in the Philippines is, as far as I know, dioecious, androdioecious or, perhaps, hermaphroditic. In most instances, three different specimens are necessary for a complete understanding of a single taxon. In *Ternstroemia toquian* only perfect flowers have been observed, and, since I have had an opportunity to examine considerable material, it may be that this type of flower is the only type for the taxon. In *T. philippinensis* var. *philippinensis* the plants are dioecious and both types have now been studied and presented here. In *T. philippinensis* var. *megacarpa*, also dioecious, only pistillate flowers and fruit have been studied. The much misunderstood *T. urdanatensis* is androdioecious. In this taxon, fortunately, both staminate and pistillate flowers were available. The pistillate flowers have well-developed stamens but these are much reduced in number. The pistillate flowers of *T. gitingensis* are still undescribed, only staminate flowers and fruit being available at this time.

Seldom have specimens in this group been collected at anthesis or near anthesis. Either fruiting specimens or those with flower buds constitute the extent of the material available. In a way, this is understandable, for the petals of fully mature flowers tend to separate from the flower and

drop quickly, usually in a single day, taking with them the attached stamens leaving only the calyx and pistil. Furthermore, the buds are so large and so tightly enclosed that when present they are often mistaken for fruits. Many of the early collections were made by native collectors who were very inexperienced.

The collections made by these collectors had been given herbarium numbers and these numbers when cited in the present paper have the initials of the herbarium between the collector's name and the number. The initials used in this paper are PBS (Philippine Bureau of Science), PBF (Philippine Bureau of Forestry) and PNH (Philippine National Herbarium).

The description below applies to the entire genus, the portions inapplicable to the species of the Philippine Islands being enclosed in brackets.

Ternstroemia Mutis ex Linnaeus f. Suppl. Pl. 39. 1781.

Flowers androdioecious, dioecious, hermaphroditic. Sepals 5, imbricate, persistent. Petals 5, connate at the base, free or joined to the middle; stamens 15–∝, 2–several-seriate, rarely 1-seriate; filaments connate, the outer adnate to the base of the corolla; anthers oblong or linear, usually shorter than the filaments, dehiscing longitudinally, the connective usually projected into an apiculate or caudate appendage, rarely muticous. Ovary 2[3, rarely 1]-loculate, the ovules in each locule 2–16, rarely solitary, pendulous from the apex of the placenta on more or less evolute funiculi. Style 1, entire or 2[or 3]-parted; stigma or stigmata punctiform or evolute, entire or lobate. Fruit irregularly dehiscent, often explosively so. Seeds usually 4, rarely 2–16; testa opaque, smooth, rarely plicate-rugulose, yellow, usually covered with reddish, many-celled papilli; endosperm pulpy, ± developed, seldom lacking; embryo bent nearly double, oily, with half-terete or flat cotyledons.

Glabrous trees, shrubs, lianas or epiphytes, with branches usually verticillate or subopposite. Leaves spirally disposed, congested or verticillate at the apex of the current year's growth, usually coriaceous, rarely chartaceous, entire or subentire. Flowers axillary, solitary, bracteolate, the bracteoles 2 [rarely 4], opposite or subopposite, placed immediately below the calyx, rarely with one somewhat removed and alternate on the pedicel.

TYPE SPECIES: *Ternstroemia meridionalis* Mutis ex Linn. f.

KEY TO THE SPECIES

1. Fruits huge for the genus, 6 cm. long, 4–5 cm. diameter, orange-red in color.
   2. Pedicels measuring up to 4 cm. long; bracteoles quickly caducous. . . . . *T. philippinensis* var. *philippinensis*.
   2. Pedicels much longer, usually about 10 cm. long; bracteoles persistent, foliaceous. . . . . *T. philippinensis* var. *megacarpa*.
1. Fruits much smaller, 1–2.5 cm. long, 1.5–2.5 cm. diameter, yellow, orange-yellow or reddish yellow.

2. Fruit and ovary 2-locular, many seeded (16–24) and multiovulate. . . . . *T. urdanatensis.*

2. Fruit and ovary 2-locular, few seeded (2–4) and pauciovulate.

3. Bracteoles 2, persistent, alternate, 5 mm. from each other below the calyx; leaves generally acute at the apex. . . . . *T. toquian.*

3. Bracteoles 2, quickly caducous, opposite, immediately below the calyx; leaves generally rounded at the apex, occasionally emarginate. . . . . *T. gitingensis.*

Ternstroemia philippinensis Merrill, Philipp. Jour. Sci. Bot. 11: 196. 1916; Enum. Philipp. Fl. Plts. 3: 72. 1923. — Melchior, Nat. Pflanzenfam. ed. 2. 21: 142. 1925.

T. philippinensis var. **philippinensis**

Tree 15–18 m. high; branchlets terete, grayish brown, 5–7 mm. diameter. Leaves thick-coriaceous, near the ends of the branchlets, generally not verticillate, oblong-oblanceolate, occasionally oblong-obovate, 12–25 cm. long, 4–7.5 cm. wide, broadly acuminate at the apex, cuneate at the base, the midrib canaliculate above, elevated below, the primary veins ca. 12 pairs, quite indistinct, usually arching upward near the margin, finally anastomosing, the petiole sturdy, 1–3 cm. long. Plants dioecious. Staminate flowers solitary; pedicel 1.5–2.5 cm. long, thick, swelling at apex to 5 mm. diameter; bracteoles 2, opposite, about 4 mm. below calyx, quickly caducous, dropping off before anthesis; no mature flowers available, the flower buds compact, ca. 1.2–1.5 cm. diameter; calyx lobes 5, rounded, very much (4 mm.) thickened at base, unequal, steadily increasing in size from the outer to the innermost lobe, the two outer 5–6 mm. long, 6–7 mm. wide, the three inner measuring 7 × 8 mm., 8 × 11 mm. and 10 × 12 mm.; petals 5, somewhat thickened (5 mm. at center), large, rounded, 2.5 cm. long, 2 cm. wide; stamens many, ca. 120 (closely attached in bud, probably more than 120), seemingly 4-seriate, unequal, the largest ones 8 mm. long, the filament 2 mm. long, joined at the base and adnate to the base of the corolla, the anthers 4 mm. long, the projection acuminate, 2 mm. long; ovary vestigial. Pistillate flowers solitary; pedicel, bracteoles, calyx and corolla as in staminate flowers; staminodia vestigial, ca. 2 mm. long, arranged in a band at the base of the pistil; ovary somewhat conical ca. 4 mm. long, 5 mm. diameter at base, 2-loculate, usually 2 ovules in each locule, the style ca. 2 mm. long, stout, divided into two parts, each part topped by a capitate-peltate stigma with irregular digitate projections. Fruit red or orange, ovoid to globose, unusually large, up to 6 cm. long and 5 cm. diameter, usually rounded at the apex, occasionally double-beaked because of the strong, separated persistent styles; seeds 4, large, up to 5 cm. long and 2.5 cm. diameter, filling the fruit cavity, covered with an orange-red mealy aril; calyx-lobes persistent, thin as in flower, separated from the fruit by a noticeable spongy thickening.

VERNACULAR NAMES: "Arana (Bik.); barañgoi (Tag.); hindang (S. L. Bis.); pamintugon (S. L. Bis.)," *fide* Merrill.

DISTRIBUTION: Luzon, Mindoro, Samar, Sibuyan.

Luzon: PROV. ILOCOS NORTE: Mt. Palimlim, *M. Ramos* PBS *33302* (A), Aug. 1918. PROV. ZAMBALES: Mt. Marayep, *M. Ramos & G. Edaño* PBS *44811* (A, BO), Dec. 1924. PROV. QUEZON: Mapatong, Tagkauayan, *M. Lagrinas* PNH *39422* (A), May 29, 1959. PROV. RIZAL: Montalban, *A. Loher 13806* (A), Jan. 1914; Mt. Sumutan, *M. Ramos & G. Edaño* PBS *29773* (A, BO), July 1917. PROV. LAGUNA: *C. Mabesa* PBF *26784* (A), Feb.–Apr. 1917; San Antonio, *M. Ramos & G. Edaño* PBS *23794* (A, BO, GH, L), Oct. 1915. PROV. CAMARINES: Mt. Bagacay, *M. Ramos & G. Edaño* PBS *33841* (A), Nov.–Dec. 1918. **Mindoro:** Paluan, *M. Ramos* PBS *39642* (A, BO, L), Apr. 1921; Pinamalayan, *M. Ramos* PBS *41070* (A, BO, L), June 1922; Mt. Halcon, *G. Edaño* PNH *3376* (L), Jan.–Feb. 1948. **Sibuyan:** PROV. CAPIZ: Magallanes (Mt. Giting-giting), *A. D. E. Elmer 12296* (A, BO, L), Apr. 1910. **Samar:** Mt. Capotoan, Catubig River, in damp soil on forest slopes, alt. 100 m., *M. Sablaya 78* (A), Feb. 20, 1916 (tree 18 m.).

Twenty-four specimens have been available for the present study of this species; of these, sixteen possessed fruit while thirteen had tight buds. In some instances buds and fruit were found on the same specimen. However, in no instance was there open flowers — or flowers near anthesis. Apparently, mature flowers of the species have never been collected. In the original citation, Merrill recorded eight numbers. In his description he mentioned only the bud, which he obviously failed to dissect, since he made no mention of the floral parts within the calyx. My own dissections for this taxon were made necessarily from buds. They are, of course, very unsatisfactory because the mature measurements cannot be ascertained. Even so, the characters which may be used in preparing a key are presented here for the first time.

Furthermore, with the exception of a single specimen (*Sablaya 78*), no field notes were recorded with the specimens studied. Perhaps the original specimens which were deposited in the Philippine herbarium possessed field notes but they have been destroyed. Sablaya recorded the species as a tree 18 m. high growing at an altitude of 100 m. in damp soil on forest slopes. Merrill reported it to be a tree 15 m. occurring "in the virgin forest at altitudes varying from 15 to 1,200 meters, depending on the region in which it grows."

The species has a rather widespread distribution (for one of this genus), extending from the northernmost province of Luzon, Ilocos Norte, south through the provinces of Zambales, Quezon, Rizal, Laguna, and Camarines, and into the islands of Mindoro, Sibuyan, and Samar.

Characteristic of *Ternstroemia philippinensis* is the very large fruit measuring 6–7 cm. in length and about 5 cm. in diameter. The leaves vary considerably in size, from quite narrow (oblong-oblanceolate) to broad (oblong-obovate). The former type has a long-acuminate apex, whereas in the latter the apex is quite rounded and bluntly acuminate. A gradation

between these two extremes can be found, and occasionally both types are found on the same branchlet.

In the specimens from the islands south of Luzon the leaves tend to be larger and obovate, similar to those found in var. *megacarpa*.

Merrill, in his initial treatment of this species, separated it from *Ternstroemia megacarpa* on the basis of "its somewhat smaller leaves and its much shorter flowering and fruiting peduncles." Evidently at the time Merrill already had prepared the manuscript for *T. megacarpa*, although the treatment for the latter species actually did not appear until two years later (1918). Since Merrill did not dissect the flower buds of *T. philippinensis*, he did not realize that the pistillate flowers were nearly identical with those of *T. megacarpa*. He made no reference to staminate flowers in either species, although from his description of *Ternstroemia megacarpa* I think that the flowers he examined were staminate.

Ternstroemia philippinensis Merrill var. **megacarpa** (Merrill), comb. nov.

Ternstroemia megacarpa Merrill, Philipp. Jour. Sci. Bot. **13**: 309. 1918; Enum. Philipp. Fl. Plts. **3**: 71. 1923. — Melchior, Nat. Pflanzenfam. ed. 2. 21: 142. 1925.

Tree about 12 m. high; branches grayish brown, terete, roughened by leaf-scars 5 mm. in diameter, the young branchlets smooth. Leaves coriaceous, oblong-obovate, large, 15–40 cm. long, 7–12 cm. wide, broadly acuminate at the apex, cuneate at the base, the midrib canaliculate on the upper surface, elevated below, the primary veins 10–15 pairs, anastomosing near the margin, the interspersed secondary veins not reaching the margin, the petiole sturdy, ca. 2 cm. long. Staminate flowers not seen. Pistillate flowers solitary; pedicel 6–10 cm. long, quite slender; bracteoles 2, alternate, foliaceous, linear, 5–8 mm. long, ca. 2 mm. wide at the base, the lower bracteole ca. 6 mm. below the calyx; calyx lobes unequal, the outer two ovate, ca. 8 × 8 mm., the inner three rounded, 9–10 mm. long, ca. 10 mm. wide; corolla in bud measuring 1–1.2 cm. across, the petals rounded, ca. 1.5 cm. long, 1 cm. wide; staminodia in several series at the base of the ovary, very small (1.5 mm.), undeveloped; ovary broadly conical, 2-loculate, 2(?) ovules in each locule; style short, 2–3 mm. long, divided into two parts nearly to the base, the stigmas peltate, 3 mm. across at center, flaring out palmately, with a fimbriate margin. Fruit yellow, ovoid, large, ca. 6 cm. long and 4 cm. across, 2-loculate, 2–4-seeded. Seeds oblong, rounded at both ends, ca. 3 cm. long, 1.5 cm. across, covered with a red mealy aril when fresh, orange-brown when dried.

VERNACULAR NAME: "Baletis (P. Bis.)," *fide* Merrill.

DISTRIBUTION: Mindanao.

Mindanao: Lanao District, Lake Lanao, Camp Keithley, *Mrs. M. S. Clemens s.n.* (lectotype, BO), Sept.–Oct. 1907, *959* (A), March 1907; Bukidnon Subprov., Tangculan and vicinity, *M. Ramos & G. Edaño* PBS *39047* (A), June–July 1920.

Even though I consider the present taxon to be only a variety of *Ternstroemia philippinensis* I have endeavored to record as complete a description as possible from the available material, which was in itself exceedingly sparse. Most of the description is supplementary to that of Merrill which seems to be lacking in most details. One must presume that Merrill examined staminate flowers from the type, *Clemens s.n.*, since he makes no mention of the pistil. He records the anther measurement as "about 1.5 cm. long." I cannot but feel that there is a mechanical error in this record, since among all the members of the genus which I have examined I have never encountered stamens, not to mention anthers, approaching this size. A more likely measurement for the anther would be 1.5 mm. Furthermore, I cannot understand why Merrill, if he was examining a staminate flower, neglected to record the measurement of the corolla, since the stamens always are adnate to the base of the corolla. In the pistillate flowers, on the other hand, the staminodia (which might measure 1.5 cm. in toto) may be found in a ring below the pistil unattached to the corolla. Although I have examined duplicates of both of Clemens' specimens cited by Merrill in the original diagnosis, no flowering material of *Clemens s.n.* was available for dissection; the fruiting specimen (*Clemens 959*) was more satisfactory.

The pistillate material used in the above description was supplied from *Ramos & Edaño 39047*. Even here, only two pistillate buds could be taken without destroying the value of the specimen. There were no mature flowers. Only the outermost petal could be removed intact and this measured ca. 1.5 × 1 cm. (In an open flower the innermost petal is usually larger than the outermost one.) The staminodia were minute and many, in several series, with the parts indistinguishable. The stigma in the first bud examined was as described above, that is, in two parts, each part palmate in shape with a fimbriate margin. In the second bud, from the same specimen the two parts of the style were further divided into two and three parts respectively, making a total of five styles, each with a flaring stigma much less in area, of course, than those found in the first bud.

From the material examined, this variety does not appear to be far removed from true *Ternstroemia philippinensis* var. *philippinensis*. The only characters which I can find which are truly different are (1) the long pedicel (up to 10 cm. long), and (2) the persistent, foliaceous, alternate bracteoles. In var. *philippinensis* the pedicel measures approximately 4 cm. in length and the bracteoles are quickly caducous. If available, they might prove to be foliaceous as in this species. These two characters hardly warrant specific delimitation.

Ternstroemia urdanatensis (Elmer) Kobuski, Jour. Arnold Arb. **28**: 46. 1947.

Adinandra urdanatensis Elmer, Leafl. Philipp. Bot. **8**: 2837. 1915, "*urdanatense*." — Merrill, Enum. Philipp. Fl. Plts. **3**: 73. 1923. — Melchior, Nat. Pflanzenfam. ed. 2. **21**: 144. 1925.

Ternstroemia epiphytica Elmer ex Merrill. Enum. Philipp. Fl. Plts. 3: 73. 1923, in syn.

Scandent shrub, epiphytic bush or lofty tree 20 m. or more high, the trunk often a meter in diameter, the main branches rising from above the middle, terete, the branchlets erect or ascending subverticillate, quite short, light gray. Leaves subverticillate, near the apex of the branchlets, coriaceous, obovate, 6–10 cm. long, 2–4 cm. wide, obtuse or somewhat rounded at the apex, cuneate at the base, the midrib canaliculate above, elevated below, the veins 5–7 pairs, quite obscure on both surfaces. Plants androdioecious. Staminate flowers axillary, solitary; pedicel 2–2.5 cm. long, slender; bracteoles 2, opposite, immediately below the calyx, persistent, deltoid, ca. 2 mm. long, 1.5 mm. wide at base, tapering to apex, ridged along the middle on the dorsal surface; calyx-lobes unequal, the two outer rounded-ovate, ca. 5 mm. long, 5 mm. wide near the base, the margin glandular, the three inner lobes obovate, ca. 6 mm. long, 4 mm. wide near the apex, glandular-margined; corolla-lobes quite equal, obovate, subunguiculate, quite membranaceous, not thickened at center, ca. 6 mm. long, 5–6 mm. wide; stamens bi-seriate(?), 100+, ca. 4 mm. long, the filaments 2.5 mm. long, very filamentous, tangled, adnate to the base of the corolla, the anthers 1.5 mm. long; pistillodium vestigial. Pistillate flowers axillary, solitary; pedicel decidedly recurved, 1.5–2 cm. long; bracteoles 2, opposite, immediately below the calyx, unequal, the outer one rounded-ovate, 2 mm. long and wide, apiculate, the inner one larger, ovate, 3–3.5 mm. long, 2 mm. wide, apiculate; calyx and corolla as in the staminate flower; stamens tangled and similar to those of staminate flower but fewer (ca. 45) in number; ovary subglobose, ca. 3 mm. long, 2 mm. diameter, 2-loculate, each locule multiovulate (ca. 14), tapering at the apex into a style ca. 3 mm. long, separated at the apex into two branches for 1 mm. or more, each branch topped by an asymmetrically globose stigma. Fruit globose, small, 1–1.5 cm. diameter, yellowish green, 2-loculate, each locule 8–12-seeded; seeds small, distorted in shape by crowding, ca. 4 mm. long and 3 mm. diameter, covered with a tawny mealy aril; fruiting style short, ca. 2 mm., split into two parts for 1 mm., the stigmas subglobose.

VERNACULAR NAME: "Sangnauan (Mbo.)," *fide* Merrill.

DISTRIBUTION: Luzon, Palawan, Mindanao.

Luzon: PROV. BATANGAS: *C. Mabesa* PBF *28051* (A), Apr. 1920. PROV. TAYABAS: Lucban, in forest, alt. 900 m., *A. D. E. Elmer 7438* (A, BO), May 1906 (tall tree climber, fls. yellow, rare); same locality, *A. D. E. Elmer 9214* (A, BO, L), ("scandent clear to top of 18 m. high tree in woods at 850 meters, branches numerous and forming bushes," flowers recurved, creamy white), May 1907; *Alcazir & G. Edaño* PNH *4537* (A), May 1939. PROV. SORSOGON: Irosin (Mt. Bulusan), *A. D. E. Elmer 15851* (A, BO, GH, L), Apr. 1916, and *17317* (A, BO, GH, L), Sept. 1916; Bulusan volcano, *M. Ramos* PBS *23671* (A), Sept. 1915. **Palawan:** Malasgao River, Aborlan, *G. E. Edaño* PNH *14028* (A, L), Mar.–Apr. 1951. **Mindanao:** PROV. AGUSAN: Cabadbaran, Mt. Urdaneta,

forested ridge of Cawilanan peak at 1700 m., *A. D. E. Elmer 14078* (lectotype of *Adinandra urdanatensis*, A; isotypes FI, GH), Oct. 1912; Cabadbaran, Mt. Hilong-hilong, mossy forest ridge, alt. 1050 m., *D. Mendoza & P. Convocar* PNH *10753* (A, L) (epiphytic bush, 2 m.), Apr. 19, 1949. PROV. DAVAO: Mt. Kampalili, at summit, alt. 750 m., *G. E. Edaño* PNH *11585* (A, L), Mar. 23, 1949 (woody vine); Camaguin de Mindanao, *M. Ramos* PBS *14595* (L), Mar.–Apr. 1912.

This taxon is the most innocuous, most often misinterpreted and misdetermined, and most difficult to understand, of any of the genus in the Philippine Islands. Although field notes were often absent from the specimens examined in this study, enough were included with this taxon to show a rather variable habit. It has been described from Luzon as "scandent clear to the top of 18 m. high tree," and "tall tree climber," and from Mindanao as "epiphytic bush 2 m.," "woody vine," or "lofty tree 20 m. high or higher."

Described originally as an *Adinandra*, this plant has been known as *A. urdanatensis*, *A. scandens*, and *Ternstroemia epiphytica*. It also resembles *Cleyera japondica* var. *montana* (originally described as *Adinandra montana*) and in many respects, it is similar to members of that genus. The fruit is relatively small and possesses a rather large number of seeds (16–24), which are small, crowded and distorted, as is often the case in *Adinandra*. The species was based entirely on a fruiting specimen. However, the locules of the fruit are definitely two in number, as in almost all the taxa of *Ternstroemia*. In *Adinandra*, the locules of the fruit number three or five. The compactness and the size of the seeds (large for *Adinandra*) resemble those found in most of the three-loculate species of *Adinandra*. The presence of staminate flowers also excludes the taxon from *Adinandra* in which all flowers are perfect. The anthers in *Adinandra* are hispid or setose, but in this species the anthers are glabrous, typical of *Ternstroemia*.

The so-called pistillate flowers in this species are in reality hermaphroditic. The stamens, although less than half the number, are similar in all respects to those found in the staminate flowers. However, there seems to be no definite serial arrangement of the stamens here even though they number only about forty-five. As many as seventeen stamens may be found on one petal, with the filaments attached to the base of the petal, while on another petal in the same flower as few as five may be found similarly attached. The style in the flowers which I examined was approximately 3 mm. long and was divided for about one-third the distance from the apex. It is doubtful that the measurement of this division has any significance other than that the style is not entire. In later development, the style may split to the base or nearly so. The stigmas are described above as "asymmetrically globose." Actually, they resemble the end of a golf club.

Ternstroemia toquian (Blanco) Fernandez-Villar, Noviss. Append. Fl. Philipp. 19. 1880. — Vidal, Rev. Pl. Vasc. Filip. 55. 1886. — Merrill, Philipp. Jour. Sci. 1: suppl. 95. 1906. — Merrill & Rolfe, Philipp.

Jour. Sci. Bot. 3: 113. 1908. — Merrill, Spec. Blancoanae 19, 264. 1918; Enum. Philipp. Fl. Plts. 3: 72. 1923. — Melchior, Nat. Pflanzenfam. ed. 2. 21: 142. 1925.

Llanosia toquian Blanco, Fl. Filip. ed. 2. 319. 1845.
Ternstroemia lobbiana Pierre, Fl. For. Cochinch. 2: sub. *t. 128.* 1887.
Taonabo toquian Merrill, Philipp. Isl. Bur. Govt. Lab. Publ. 27: 21. 1905.

Slender tree 5–10 m. high, branching usually at the apex only; branches gray-brown, terete, subverticillate. Leaves coriaceous, crowded at the apex of the branchlets, obovate, 5–8 cm. long, 1.5–2.5 cm. wide, abruptly acuminate at apex (definitely rounded in specimens from Ilocos Norte and Cagayan), cuneate at base tapering gradually and decurrently into a petiole less than 1 cm. long, the midrib canaliculate above, elevated below, the veins (3 or 4 pairs), inconspicuous on both surfaces. Flowers hermaphroditic (as far as known), solitary, axillary; pedicel 2.5–3 cm. long; bracteoles 2, alternate, 5 mm. distant from each other below calyx, ovate, 1.5 × 1.5 mm., subacute at the apex, glandular-apiculate; calyx-lobes unequal, joined at the base more than in most species, thickening in fruit, the two outer lobes rounded, ca. 3 mm. long, 3.5 mm. wide, the inner lobes about as long as the outer lobes but wider, 5 mm. wide, the margin scarious; corolla-lobes unequal, the outer ones obovate, 10–11 mm. long, 5–6 mm. wide, broadly obtuse at the apex, narorwed at the base, the margin lightly scarious, progressively so in the inner ones, the inner one ca. 10 mm. long, about the same as the outer ones, wider, 8–10 mm. also wider at the base, rounded at the apex, the margin quite scarious; stamens several-seriate, crowded, mounted on a disk which is raised toward the center, ± 175, free from the petals, ca. 3.5 mm. long, the filaments joined lightly at the base, ca. 1.5 mm. long, the anthers ca. 1.25 mm. long, the projection 0.25 mm. long, subemarginate; ovary conical, 2-loculate, with three or more ovules in each locule attached at the apex of the cell, the style negligible, only 0.2 mm. long, divided into two parts, the stigmas 2, fan-shaped with scalloped edges, spreading over the apex of the ovary. Fruit globose, 2–3 cm. long, about the same in diameter, thin-shelled, orange-yellow, 2-loculate, occasionally appearing 1-loculate (because of broken septum), each locule one- or two-seeded, the seeds 1–1.7 cm. long, ca. 1 cm. diameter, covered with a tawny or orange aril.

VERNACULAR NAMES: "Bigag (Tag.); bikag (Tag.); boalau (Mbo.); debaak (Ilk.); garamansatai (Tag.); malapuyau (Tag.); simbinuluka (Sbl.); tabak (Ilk.); tokian (Tag.)," *fide* Merrill. "Batohan-no-mahing-tig, Boalau," *fide* Elmer.

DISTRIBUTION: Luzon, Mindoro, Sibuyan, Panay, Palawan, Mindanao.

Luzon: PROV. ILOCOS NORTE: Bangui, *M. Ramos* PBS *27417* (A, BO), Feb.–Mar. 1917. PROV. ILOCOS SUR: *E. Paraiso* PBF *25463* (A), Mar. 1918. PROV. CAYACAN: Lucban, Abulog, in swampy places, *V. Veracion* PNH *33432* (L), Jan. 2, 1955; *H. M. Curran* PBF *17205* (BO), Mar. 1909; Mt. Bababtning, *G. Edaño* PBS *79395* (BO), May 1930. PROV. BENGUET: *M. Ramos* PBS *5596* (BO, L), Dec. 1908. PROV. PANGASINAN: Mt. Isidro, *E. Fenix* PBS *29966* (BO,

GH, L), Nov. 1917. PROV. ZAMBALES: Mt. Tapalao, *M. Ramos & G. Edaño* PBS *44727* (A), Nov.–Dec. 1924; *M. Ramos* PBS *4795* (BO, GH), Dec. 1907. PROV. ECIJA: Carabbala Mts., *S. Vidal y Soler 58* (A, L); *R. J. Alvarez* PBF *22149* (BO), Dec. 1910. PROV. PAMPANGA: Mt. Arayat, *E. D. Merrill 5021* (L), Feb. 1906; Mt. Arayat, *E. D. Merrill* Sp. Blanco. *720* (BO, GH, L). PROV. BATAAN: Mt. Mariveles, Lamao River, *T. E. Borden* PBF *787*, *835*, *2935* (BO), 1904–1905, *R. Meyer* PBF *2605*, *2614*, *2760* (BO), Feb. 1905, *P. T. Barnes* PBF *150* (BO), Jan. 1904, Ahern's Coll. PBF *1506* (BO), July–Aug. 1904; Upper Lamao River, alt. 1000 m., *R. S. Williams 403* (GH), Jan. 3, 1903 (tree 10 m. high); Mt. Kuyapo, *G. Edaño* PNH (L), Nov.–Dec. 1947; *A. P. Racelis* PBF *27987* (BO), Feb. 1920; Mt. Mariveles, mountains above 700 m. alt., *P. T. Barnes* PBF *208* (A), Jan. 1904 (small tree). PROV. BULACAN: Angat, *S. Vidal y Soler 59* (A, L). PROV. RIZAL: Mt. Lumutan, *M. Ramos & G. Edaño* PBS *29703* (GH), July 1917; Tanay, *E. D. Merrill 2288* (GH), May 1903; *A. Loher 13895* (A), Jan. 1913; Paningtinan, *A. Loher 13482* (BO), Mar. 1915. PROV. LAGUNA: Mt. Banahao, *S. Vidal y Soler 58c* (A). PROV. TAYABAS: *G. Edaño* PBS *26900* (L), Mar. 1917; Mt. Camatis, *Alcazir & G. Edaño* PNH *4541* (A), May 1929. PROV. CAMARINES SUR: Kamugong River, *G. Edaño* PBS *75846* (BO), Oct. 1928; Sarapan, *G. Edaño* PBS *76141* (A), Oct. 1920. **Mindoro:** Paluan, *M. Ramos* PBS *39755* (A, BO, L), Apr. 1921. **Sibuyan:** Magallanes, Mt. Gitinggiting, in moist, rocky soil of forested ridge, alt. 800 m., *A. D. E. Elmer 12428* (A, BO, GH, L), May 1910 (slender, erect tree 5 m. high, branched toward the top only). **Panay:** PROV. ILOILO: Miagao, Bugani, *S. Vidal y Soler 58 bis* (A). **Palawan:** Puerto Princesa, *A. L. Cenebra* PBF *29200* (A), Feb. 1923. **Mindanao:** PROV. AGUSAN: Cabadbaran (Mt. Urdaneta), in red clay on steep forested ridge, alt. 400 m., *A. D. E. Elmer 13282* (A, BO, GH, L), July 1912 (small tree 10 m. high, branched from the middle).

This taxon is the first-recognized member of the genus from the Philippine Islands and understandably so since it has by far the broadest distribution of the group in that area. It has been widely collected from the northernmost provinces of Luzon throughout the island, including (in my study) specimens from Ilocos Norte, Cayacan, Benguet, Pangasinan, Zambales, Neuva Ecija, Pampanga, Bataan, Bulacan, Rizal, Laguna, Tayabas, and Camarines Sur, sometimes with several collections from each province. The species extends southward from Luzon through Mindoro, Sibuyan, Panay, Palawan into Mindanao. With all of the specimens represented, field notes are at a minimum. Very rarely is anything but the general locality in a province given and often even that is missing.

There is considerable variation found in the leaves. Generally they are obovate in shape, with the apex abruptly acuminate, measuring 5–8 cm. in length and 1.5–2.5 cm. in width. In some specimens from Benguet Province, Luzon, the leaves are as long as 10 cm. but are still only 2.5 cm. wide, giving a much narrower appearance. From Ilocos Norte and Cayagan provinces, the leaves are definitely rounded at the apex.

Even though there is considerable variation in leaf size and shape, the following characters are quite consistent. The small calyx lobes are distinctly joined at the base in the flower in the form of a shallow cup, the united portion thickening in fruit. The style is minute, in fact so minute as to be preserved in the fruit without damage. The stamens, joined to-

gether only lightly at the base, are not attached to the petals, a character most unusual in the genus. The "disk" or base for the very many stamens (ca. 175) is raised somewhat at the center.

The flowers examined by me all proved to be hermaphroditic. There may be staminate flowers but I was unable to find any. In all dissections, the ovary proved to be two-loculate with three or more ovules in each locule. Variation in fruit development may be found. In rare instances the locule wall has broken down giving the appearance of a one-loculate fruit with two seeds. However, in such instances one can see the edges of the broken septum along the side. In most instances the fruit retains the septum and is filled with two, three, four, or even more well-developed seeds.

Ternstroemia gitingensis Elmer, Leafl. Philipp. Bot. 4: 1480. 1912, "gitingense"; Merrill, Enum. Philipp. Fl. Plts. 3: 71. 1923. — Melchior, Nat. Pflanzenfam. ed. 2. 21: 142. 925.

Ternstroemia obovata Merrill, Enum. Philipp. Fl. Plts. 3: 71. 1923, nomen.

Small tree 8–10 m. high, branching at the top, the main branches crookedly rebranched, lax, with ascending tips, yellowish gray; branchlets grayish white, ca. 5 mm. thick. Leaves verticillate at the tips of the branchlets, horizontal or radially spreading, thick-coriaceous, obovate, rounded at the apex, occasionally emarginate, cuneate at the base, (9–)12–15 cm. long, 4–6 cm. wide, reddish on the upper surface, yellowish green beneath, the midrib canaliculate above, elevated below, the veins about 4 pairs, quite obscure on both surfaces, the petiole stout, ca. 2 cm. long. Plants androdioecious. Staminate flowers solitary, axillary; pedicel 1–2 cm. long; bracteoles opposite, immediately below the calyx, quickly caducous; calyx-lobes unequal, quite thickened at the center at the base, the two outer smaller, ca. 3 mm. long, 4.5 mm. wide, rounded, with a thin margin, the three inner rounded, with an abrupt transition from thickened center to wide scarious margin, ca. 5 mm. long, 6 mm. wide; corolla-lobes rounded at apex, unguiculate, ca. 10 mm. long, 8–10 mm. wide near center, 4–5 mm. wide at base; pistillodium sterile, deceptively appearing to be fertile, conical, 2 mm. long, 2 mm. wide at base, occasionally 2-loculate, 0-ovulate, usually lacking locules; stamens ca. 120, several-seriate, very short and sturdy, nearly filling flower, 2.5 mm. long, the filament and anther each about 1 mm. long, the projection truncate before pollen dispersal, later bifid. Pistillate flower not seen. Fruit globose or ellipsoid, ca. 2 cm. long, reddish yellow, quite thin-shelled, 2.5 cm. long, ca. 1.5 cm. diameter, 2-loculate, each locule single-seeded. Seeds about 1.3 cm. long, 0.8 cm. in diameter, attached at the apex, covered with a crimson-red, mealy aril. The fruiting style very short (1 mm. or less), topped by a spreading, peltate stigma.

VERNACULAR NAMES: "Apin (Tag.); palilag (Ibn.); tapmis (C. Bis.)," *fide* Merrill.

DISTRIBUTION: Luzon, Sibuyan, Panay, Palawan.

Luzon: PROV. ISABELA: Palanan Bay, *I. Escritor 1209* (BO, GH, L), June 1913. PROV. TAYABAS: Baler, *E. Quisumbing* PNH *7654* (A), May 1941; Mt. Binuang, *M. Ramos & G. Edaño* PBS *28564* (A), May 1917. **Sibuyan:** PROV. CAPIZ: Magallanes, Mt. Giting-giting, steep, densely wooded ravine near a creek, alt. ca. 500 m., *A. D. E. Elmer 12397* (A, lectotype; BO, GH, L, isotypes), May 1910. **Panay:** PROV. CAPIZ: Libacao, *A. Martellino & G. Edaño* PBS *35448* (A, BO, L), May–June 1919. **Palawan:** PROV. PALAWAN: Puerto Princesa, Mt. Pulgar, in low, black, compact soil in a lightly wooded flat area, alt. 80 m., *A. D. Elmer 12901* (A, BO, GH, L), May 1911.

This species is the smallest fruited taxon found in the Philippines. The distribution is of a pattern which Elmer considered quite typical for the Philippines, namely, from Luzon, south through Sibuyan into Palawan.

Elmer based his original description on two of his own collections, *12397*, from Sibuyan, and *12901*, from Palawan. Since the type material in Manila has been destroyed it is necessary to designate a lectotype. I have selected *Elmer 12397* (in the Arnold Arboretum herbarium) as the lectotype. Of the two numbers cited by Elmer, *12397* is the only one with fruiting material. Furthermore, it was collected from a region centrally located as far as distribution is concerned. In his field notes Elmer refers to fruiting material on his no. *12901*. However, I have examined four duplicates of this number and have found them all sterile.

The fruits examined in this study showed them to be 2-loculate with a single seed in each locule. I doubt that this will hold as a specific character, for later fruit collections may well show two seeds to a single locule, variation in seed number being not at all unusual in *Ternstroemia*. Unfortunately, no pistillate flowers were available, hence the ovule number could not be ascertained.

The staminate flower might be mistaken for a perfect flower. The pistillodium is much more developed than is usually found in staminate flowers of the genus. It is of the size of many functional pistils, tapering, however, from the base to the apex with no definite style. In one dissection I found two distinct lacunae (or locules) but a careful search revealed no ovules. In all the other dissections there were no evidences of locules.

The leaves of the specimens from the southernmost area (Sibuyan and Palawan) are larger than those found in the northern specimens, measuring as much as 15 × 6 cm. In the Luzon specimens the leaves are smaller, measuring only 9 × 4 cm. These, of course, are the two extremes.

This species is closely allied to *Ternstroemia toquian*, the first-described species from the Islands and one much more widely distributed. Only staminate flowers and fruit were observed in *T. gitingensis*. However, a study of the styles, occasionally attached to the fruit, show that they are very short (not more than a millimeter in length) and that the fragmentary stigmas are peltate. One may presume, naturally, that the pistillate flowers when observed will bear out these characters. In *T. toquian*, on the other hand, only pistillate flowers were observed. Here, the ovary

contained 2 or 3 ovules for each locule with a very brief style and a peltate stigma. The fruit has only one or two developed seeds, however.

It may turn out eventually that *Ternstroemia gitingensis* is merely the staminate phase of *T. toquian*. However, the perfect flower of *T. toquian* has 175 stamens, while the staminate flower of *T. gitingensis* has only 120 stamens. There are a few other minor differences. In *T. toquian*, the bracteoles are alternate, 5 mm. distant from each other below the calyx, and persistent. In *T. gitingensis* the bracteoles are opposite, immediately below the calyx, and quickly caducous. The leaves in *T. toquian* are smaller, 5–8 cm. long and 2.5 cm. wide, obovate and abruptly acuminate at the apex. However, leaf shape and size are not sound characters for delimiting species in this genus. In certain specimens of *T. toquian*, the leaves are definitely rounded at the apex. In *T. gitingensis*, the leaves are larger, 12–15 cm. long, 4–6 cm. wide and always rounded at the apex, sometimes emarginate.

LEAF AND NODAL ANATOMY OF SOME ANDEAN COMPOSITAE–ASTEREAE

OTTO T. SOLBRIG [1]

ANGIOSPERM LEAVES sometimes provide valuable taxonomic characters. Superficial foliar characteristics that are readily observable, such as pubescence, leaf shape, and type of margin, are in common use and frequently provide diagnostic information. Anatomical characters, on the other hand, are used with less frequency, due partly to their greater uniformity and also to the more elaborate techniques required. Nevertheless, anatomical characters have some desirable attributes which counterbalance their relative inaccessibility in the field. The smaller degree of inter- and intraspecific variability enhances the reliability of differences and makes them more amenable to measurement and therefore more precise. Venation pattern and characters of the node are also useful as sources of information for the taxonomist. Carefully evaluated, they can be used in the interpretation of phylogenetic evolution and adaptive trends.

Phenotypic characters reflect the past evolutionary history of the plant, as well as its present environment, and it is generally agreed that phenotypic characters are adaptive (Mayr, 1942; Stebbins, 1950; Simpson, 1953). Nevertheless it is not always easy to see this, and one should beware of simple anthropomorphic or teleological explanations. Interpretations are devoid of meaning unless they are backed by careful physiological experiments. Likewise, one should avoid interpreting our ignorance about the function of a given structure as a lack of any usefulness.

Angiosperm leaves are one of the most favorable organs in which to study adaptation to diverse environments because they are connected primarily with the water economy of the plant. Adaptation of leaves to conditions of extreme drought has been studied both anatomically and physiologically. Much more study is needed, however, in order to understand the operating selective forces which account for the general adaptive trends. We will need eventually a detailed knowledge of the anatomical features of all species which grow in dry regions, as well as a detailed understanding of the complex ecological conditions which surround their growth.

This paper presents an anatomical and morphological study of the

[1] I am very grateful to Dr. Angel L. Cabrera, of the Museo de La Plata, and to Ing. Agr. Armando Hunziker, of the Museo Botánico, Córdoba, Argentina, for supplying me with critical material. Drs. Sherwin Carlquist, Lincoln Constance, Adriance Foster, Lorin I. Nevling, Jr., and Carroll E. Wood, Jr., kindly read the manuscript and made various helpful suggestions. Finally the help of the directors and curators of the Arnold Arboretum (A), the Gray Herbarium (GH), and the United States National Herbarium (US), for allowing the use of herbarium material in their custody is acknowledged.

leaves and subtending nodes of a group of twenty species in seven related genera. Since these species grow in different, although similar, environments, some insight can be obtained as to the modifications which accompanied the radiation of these species into the extreme conditions of habitats in the high Cordillera de los Andes of South America.

Two of these small genera of Compositae–Astereae are monotypic: *Lepidophyllum cupressiforme* (Lam.) Cassini occurs only in sandy or alkaline soils in southeastern Patagonia and Tierra del Fuego (Cabrera, 1945); *Aylacophora deserticola* Cabrera is known only from the type locality, Plaza Huincul, Prov. de Neuquén, in Argentina (Cabrera, 1953a). Of the other genera, *Parastrephia* Nutt. emend. Cabrera, with five species, grows on the high plateaus (known as *puna*) of southern Perú, southwestern Bolivia, northern Chile, and northwestern Argentina (Cabrera, 1945, 1954a, 1958). The three species of *Chiliotrichiopsis* Cabrera are distributed from the *puna* of northwestern Argentina to the mountains of La Rioja and Mendoza, in the south (Cabrera, 1937, 1944, 1954b). *Nardophyllum* Hook. & Arn., with seven species, occupies the widest geographical range: four species are found in central Chile and the adjacent Prov. de Mendoza in Argentina; two are frequent in Patagonia and southern Chile, ranging from Neuquén to Tierra del Fuego; and one, *N. armatum* (Wedd.) Reiche is a dominant shrub in the climax steppe of the *puna* (Cabrera, 1954a, 1958). The two species of *Chiliophyllum* Phil. have a disjunct distribution, being restricted to Mendoza (*C. densifolium*) and Tierra del Fuego (*C. fuegianum*) respectively. Both species of *Chiliotrichium* Cass. are found in central and southern Chile and neighboring areas of Argentina, from Santiago to Tierra del Fuego (Reiche, 1902). Thus these genera range from Tierra del Fuego, in the southernmost tip of South America, to the highlands of southern Bolivia, a distance of some 4000 km.

All the plants studied are woody shrubs, varying in height from 20 to 150 cm., the majority being about 50 to 100 cm. high. Although none, with the possible exception of *Nardophyllum bryoides,* can be called a true cushion plant, there is a definite tendency in that direction. The branching is dense, the plants form round mats, the leaves are short and crowded, and the inflorescences are borne on short stalks. These characters are more evident in some species than in others. It is hoped that some information may be gained from this study relative to those modifications accompanying adaptation to a pulvinate type of growth in related species.

All observations were made on herbarium specimens. Leaves were cleared according to Foster's technique as explained elsewhere (Solbrig, 1960). Sections of leaves and shoots, expanded in a 2.5% solution of sodium hydroxide for two to six hours, were prepared following the tertiary butyl alcohol method of Johansen (1940) and stained according to the safranin-fast green method (Johansen, 1940). Additional studies were made of hydrated and dried herbarium material.

Both young and mature leaves were studied. Stem material chosen for

sectioning was that of primary and usually very young shoots. More than one node was sectioned in every case. Whenever possible, shoot apices were sectioned and studied.

THE LEAF

External morphology. The leaves of all species studied are small, coriaceous, appressed to the stems or spreading, sessile, spirally arranged (with the exception of the opposite leaves of *Lepidophyllum*), densely hairy on at least one surface, with entire and usually revolute margins. Nevertheless, there are some differences in external aspect which justify description genus by genus.

Leaves of *Nardophyllum genistoides* (Phil.) Gray are linear-lanceolate, 1–1.5 cm. long and 3–4 mm. wide, glandular-pubescent, with entire non-revolute margins. All other species of the genus have linear leaves, varying in length from not more than 5 mm. in *N. bracteolatum* Hauman to almost 2 cm. in *N. chiliotrichioides* (Remy) Gray. The upper surface is glabrous or sparsely pubescent, the lower one densely pubescent. In *N. lanatum* (Meyen) Cabrera both leaf surfaces are white-pubescent. The leaf margins in all these species are strongly revolute and the surfaces are usually very resinous. In two species, *N. bryoides* (Lam.) Cabrera and *N. bracteolatum* Hauman, the leaves are densely crowded on the shoots, the internodes being less than 1 mm. in length.

Parastrephia lucida (Meyen) Cabrera and *P. phyliciformis* (Meyen) Cabrera have relatively large linear leaves, 35 mm. long and 2–4 mm. wide, horizontally curved, and very resinous,[2] with revolute margins and a pubescent lower surface. *Parastrephia quadrangularis* (Meyen) Cabrera and *P. lepidophylla* (Wedd.) Cabrera have small linear leaves, 3–5 mm. long and 1–2 mm. broad, the lower portions with clasping margins, the tips appressed to the stem, the middle and upper portions with the borders abaxially revolute and the outer surface pubescent. Finally, *P. teretiuscula* (O. Ktze.) Cabrera has small triangular leaves, 1–2 mm. long and 1–2 mm. broad, tightly appressed to the stem, with the outer surface covered with mixed glandular and nonglandular trichomes.

The leaves of *Lepidophyllum cupressiforme* (Lam.) Cassini are opposite, scale-like, appressed to the stem, crescent-shaped, about 1–1.5 mm. long and broad, glabrous and resinous. *Aylacophora deserticola* Cabrera, on the other hand, has ephemeral leaves sparsely arranged on the branches (internodes 5–15 mm. long), linear, 5–15 mm. long and 0.5–1 mm. wide, either woolly or glabrescent.

Chiliotrichiopsis Keidelii Cabrera has linear leaves 3–5 cm. long and up to 1 cm. wide, the upper surface glabrous, and the lower pubescent, with inrolled margins. *Chiliotrichiopsis ledifolia* (Griseb.) Cabrera, in con-

[2] Fries (1905) states that species of *Parastrephia* (*Lepidophyllum*) *quadrangularis* and *P. phyliciformis* are so resinous that they will readily burst into flame when a match is thrust into the green branches. I have witnessed a similar occurrence with *Gutierrezia Gayana*, a species of similar habit, growing in Chile.

trast, has lanceolate leaves about 3 cm. long and 1–2 cm. broad, the upper surface glandular-pubescent, the lower surface densely so, and the margins not inrolled.

Both species of *Chiliotrichium* have linear-lanceolate leaves that are shiny and sparsely glandular-pubescent on the upper surface, densely pubescent on the lower, and with a revolute margin. The leaves of both are approximately 1–3 cm. long, those of *C. diffusum* Dusén being somewhat broader (3–5 mm.) than those of *C. rosmarinifolium* Less. (1–2 mm.).

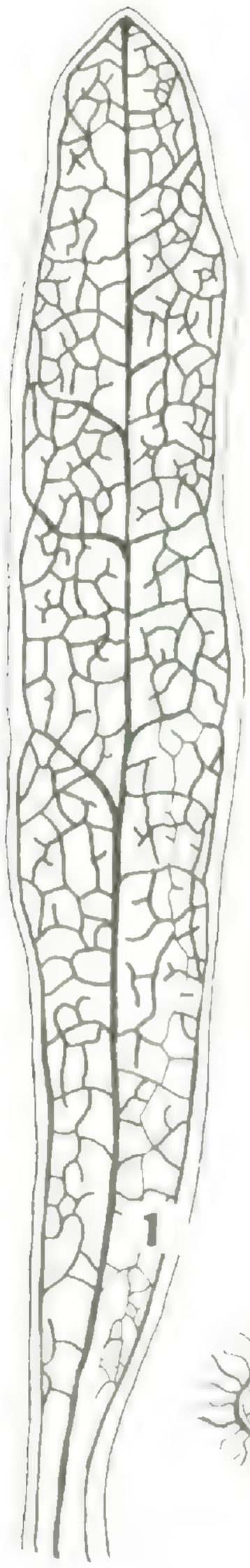
The leaves of both species of *Chiliophyllum* studied are similar to each other: *C. densifolium* Phil. has lanceolate leaves 3–5 mm. long and 2 mm. wide, glabrous on the upper surface, and only slightly glandular-pubescent on the lower; *C. fuegianum* O. Hoffm. has similar leaves 7–8 mm. long and 2–3 mm. wide.

Summarizing briefly it may be said that the leaves of all species studied show such common features as small size, pubescence, and inrolled margins, which are very much in evidence in such species as *Parastrephia teretiuscula* and *Lepidophyllum cupressiforme*, in which the leaves are reduced to small appressed scales.

Venation. The venation pattern shows variations comparable to those observed in the external aspect of the leaf. Here we see a reduced enervation of the lamina and a concomitant increase in sclerification of the veins.

The pattern is basically a reticular one, with a pronounced midvein and two approximately parallel large lateral veins, which often give rise to two more large laterals. The laterals usually are prominent only in the lower third of the lamina, becoming less and less conspicuous toward the tip. This pattern is well represented in leaves of *Chiliotrichiopsis ledifolia* and *Parastrephia lucida*. The first step in vein reduction is a decrease in the number of small veinlets. Types of this sort are the most frequent, and are to be found to varying degrees in *Nardophyllum armatum*, *N. chiliotrichioides*, *N. genistoides*, *N. bracteolatum*, *N. lanatum*, *Parastrephia phyliciformis*, *Chiliotrichiopsis Keidelii* (Fig. 1), *Chiliotrichium diffusum*, and *C. rosmarinifolium*. *Aylacophora deserticola* also possesses this general type of venation, but the veinlets are very thick because of a well-developed sheath of sclereids.

The next step in the apparent reduction series is a gradual disappearance of the two main laterals, so that only the midvein and a few of its branches are left. As we will see this step is associated with changes in the node. In *Nardophyllum bryoides*, *N. obtusifolium* Hook. & Arn. (Fig. 2), *Parastrephia quadrangularis*, and *P. lepidophylla* some traces of the laterals remain, but, on closer examination, it can be seen that they branch off the midvein near its base. In *Chiliophyllum fuegianum* (Fig. 3) and *C. densifolium* (Fig. 4), no trace remains of the laterals, for only the midvein and a few branches, which are highly sclerified in *C. densifolium*, are left. In *Lepidophyllum cupressiforme* and *Parastrephia teretiuscula* (Fig. 5) there occurs lateral development of the reticulum, giving an almost peltate appearance to the lamina. Both species have a well-developed sheath of sclereids surrounding the midvein and the veinlets.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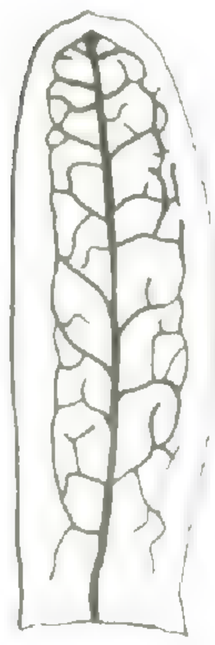
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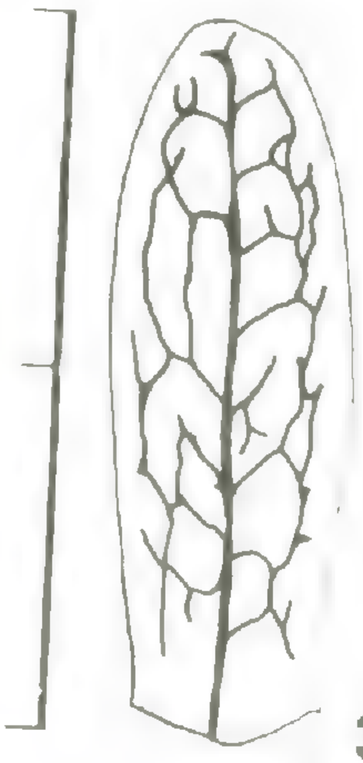
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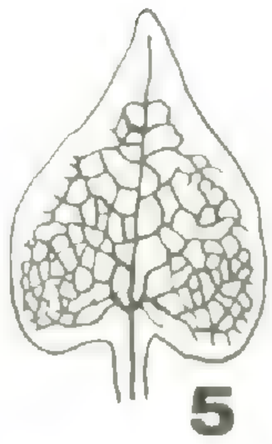
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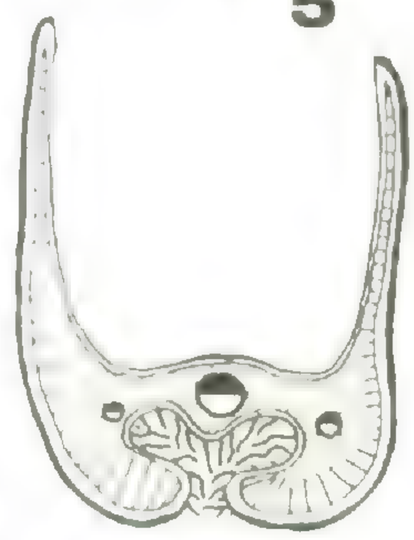
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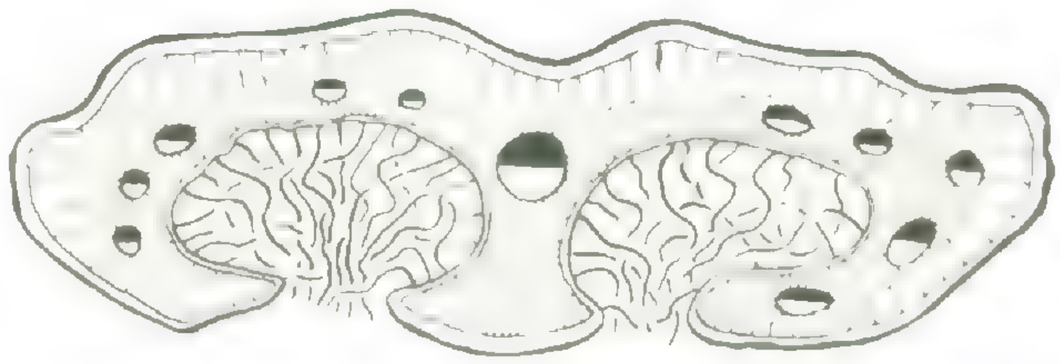
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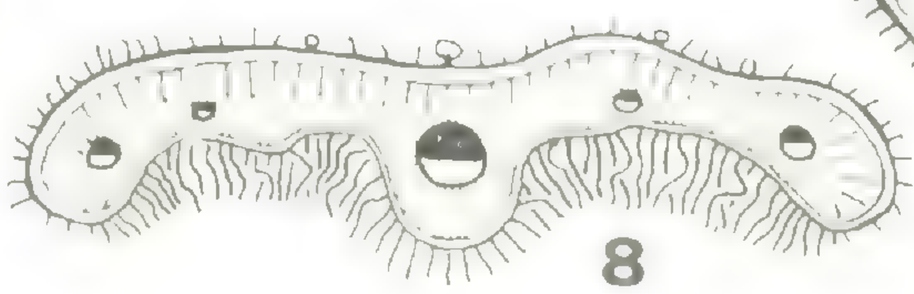
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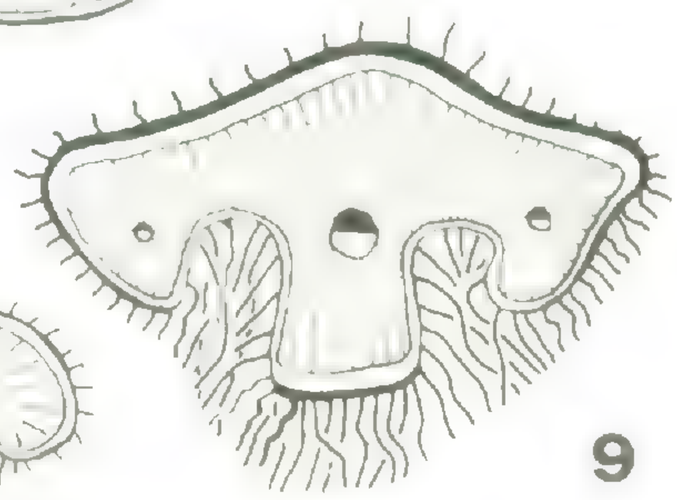
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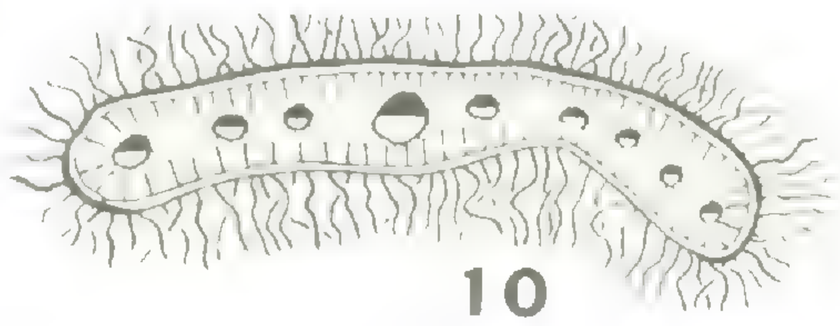
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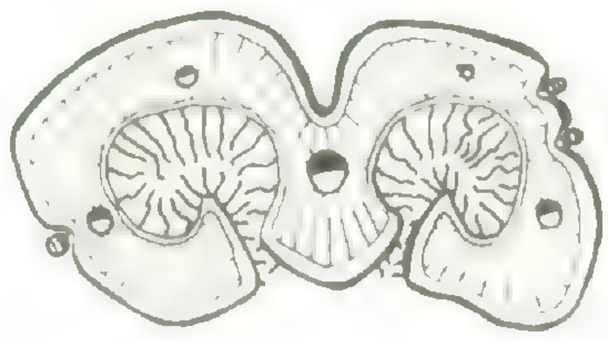
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FIGS. 1–6. Leaf venation. Veins in black, differences in width due to sclerenchyma. Each division of scale equals 1 mm. 1, *Chiliotrichiopsis Keidelii* (*Venturi 3012*, A); 2, *Nardophyllum obtusifolium* (*Pirion 3360*, GH); 3, *Chiliophyllum fuegianum* (*J. Hunziker 6827*, LP); 4, *Chiliophyllum densifolium* (*Serra 70*, LP); 5, *Parastrephia teretiuscula* (*Cárdenas 86*, GH). FIGS. 6–12. Leaf cross sections. Hairs and glandular hairs represented schematically; cuticle indicated by thick black line, differences in thickness reflecting actual differences; epidermis a white band; palisade parenchyma by horizontal bars; and spongy

Anatomy. The general plan of leaf construction is quite similar in all species studied, as might be expected in closely related genera and species. There are, however, a number of significant differences which will be treated in detail.

For purposes of clarity, four general types will be described; it must be kept in mind, however, that these are artificial and without any evolutionary or phylogenetic significance *per se*.

TYPE A. This might be called the "ericaceous type," because of its similarity to the leaves of certain species of Ericaceae (Hagerup, 1953). The most characteristic features are the strongly inrolled margins and the well-developed midvein region which protrudes considerably on the abaxial surface and forms in connection with the inrolled margins two longitudinal "inner cavities" along the surface of the leaf. These cavities are covered with a very dense mass of hairs (FIG. 20). The general outline in cross section is like that of two contiguous U-beams. This general situation is found in *Nardophyllum bryoides* (FIGS. 25–27), *N. obtusifolium* (FIG. 9), *N. armatum*, *N. bracteolatum*, *N. chiliotrichioides* (FIG. 11), *Parastrephia lucida* (FIGS. 13, 20), *P. phyliciformis* (FIG. 15), and *Chiliotrichium rosmarinifolium*.

In all these species there is a very thick cuticle, sometimes almost as thick as the epidermis itself, and the epidermis is always simple and composed of large to very large cells. The thick epidermal layer covers the whole upper surface and the outer sides of the inrolled margins (which can present a considerable surface); in addition, it often covers the exposed area of the downward-protruding midvein region. Beneath the epidermis are one to three layers of tightly appressed palisade parenchyma, which occupy about one-half the thickness of the leaf, including the sides. The other half, which faces the "inner cavity," is occupied by one to several layers of spongy parenchyma. The epidermal layer lining the "inner cavity" is relatively thin. Uniseriate multicellular hairs, common in Compositae (Metcalfe and Chalk, 1950) are universally present in great profusion in the "inner cavity" and on the upper leaf-surface with varying degrees of density; so also are multicellular, multiseriate glandular hairs (FIGS. 26, 27). The vascular strands in all the leaves, regardless of type, are collateral, and the larger ones are often surrounded by a fibrous sheath. A more detailed description of the vascular bundles will be given later.

The other three leaf types could be interpreted as modifications of Type A, derived by a gradual "unfolding" of the margins. Two different trends or "lines" can be inferred for purposes of description only, since there is no evidence at all to indicate a direct descent, a possibility which indeed seems unlikely.

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parenchyma by stiples; outline of leaves drawn with camera lucida. Each division of scale equals 0.1 mm. 6, *Chiliotrichiopsis Keidelii* (*Fabris & Marchioni 1748*, LP); 7, *Parastrephia lepidophylla* (*West 7138*, GH); 8, *Nardophyllum lanatum* (*Morrison & Wagenknecht 17123*, GH); 9, *Nardophyllum obtusifolium* (*Pirion 3360*, GH); 10, *Aylacophora deserticola* (*Cabrera 11053*, LP); 11, *Nardophyllum chiliotrichioides* (*Morrison 17321*, GH); 12, *Chiliotrichium diffusum* (*Eyerdam, Beetle & Grondona 24098*, GH).

TABLE I. Principal foliar anatomical characteristics

	LEAF POSITION	LENGTH MM.	WIDTH MM.	MARGINS	CUTICLE μ	EXPOSED EPIDERMIS μ	PALISADE LAYERS	SPONGY LAYERS	LEAF TRACES
Nardophyllum									
genistoides	horizontal	10–15	3–4	curved	*	*	*	*	3
chiliotrichioides	horizontal	10–20	1–2	convolute	4.5–7.5	13.5–15	1	2–4	3
lanatum	horizontal	5–10	1–2	convolute	6–7.5	15–22.5	1	1–2	3
bracteolatum	horizontal	12	1.5	convolute	1.5–3	22.5–30	1–2	2–4	3
obtusifolium	horizontal	3–4	1	convolute	1.5–4.5	12–15	1	1–3	1
bryoides	horizontal	5	1–2	convolute	1.5–4.5	12–15	2–3	2–3	1
armatum	horizontal	3–10	.5–1.5	convolute	3–4.5	18–25.5	*	*	3
Aylacophora									
deserticola	horizontal	3–10	1–2	straight	1.5? *	*	1–2	3–4	3
Parastrephia									
lucida	horizontal	35	2.5	convolute	4.5–12	18–25.5	1–2	1–2	3
phyliciformis	semiappr.	5	1–1.5	vestigial convolute	6–7.5	15–22.5	1–2	1–2	3
quadrangularis	semiappr.	3–4	1–2	convolute	13.5–16.5	15–22.5	1–2	2–4	3
lepidophylla	appressed	4–5	1–2	convolute	4.5–6	13.5–18	2–4	2–3	1
teretiuscula	appressed	1–2	1–2	curved	3–4.5	15–22.5	2–3	2–3	1
Lepidophyllum									
cupressiformis	appressed	1–1.5	1–1.5	straight	7.5–15	15–22.5	2–4	2?**	1
Chiliotrichiopsis									
Keidelii	horizontal	30–50	3–5	slightly convolute	3–4.5	10.5–15	1–2	1–2	3
ledifolia	horizontal	20–30	5–10	straight	1.5–3	7.5–9	*	*	3
Chiliotrichium									
rosamarinifolium	horizontal	10–20	1–2	convolute	6–12	10.5–15	1–2	1–2	3
diffusum	horizontal	10–20	3–5	slightly convolute	9–10.5	15–18	1–2	1–2	1
Chiliophyllum									
densifolium	horizontal	3–5	1–2	straight	1.5–3	13.5–15	1–2	3–5	1
fuegianum	horizontal	7–8	2–3	straight	4.5–6	10.5–13.5	1–2	3–5	1

* Material does not permit a precise determination.

** Spongy parenchyma consistently broken, forming a large air-filled cavity. Natural or artifact?

TYPE B. The leaves of only four species can be classed here: *Lepidophyllum cupressiforme*, *Parastrephia teretiuscula* (FIGS. 14, 21), *P. lepidophylla* (FIG. 7), and *P. quadrangularis* (FIG. 18). All four species occur under extreme environmental conditions: *Lepidophyllum* on sandy and alkaline soils in the cold southern regions of Patagonia and Tierra del Fuego, and the species of *Parastrephia* on the high *puna* above 3300 meters. The leaves of all four species are appressed to the stems in varying degrees. In *Parastrephia lepidophylla* (FIG. 7) and *P. quadrangularis* (FIG. 18) we find revolute margins and a strongly modified "inner cavity"; in *P. teretiuscula* (FIGS. 14, 21) there is only a small vestige of a

cavity, while in *Lepidophyllum cupressiforme* there is no evidence of a cavity.

It already has been mentioned that the leaves of all the species under study are sessile and slightly clasping at the base. In leaves of Type B, not only the base but the whole lower half of the leaf partially embraces the stem. The abaxial surface in *Parastrephia* presents two flanges with inrolled margins, so that a transection of the leaf taken somewhere between one-third to one-half the distance from the base resembles a modified "X" (FIG. 15). This presents the problem as to which is the true margin, a question which will be examined in connection with the ontogeny of the leaf.

The abaxial, rather than the adaxial, surface is the one here provided with a thick layer of cutin and a thick, one-layered, large-celled epidermis, subtended by a single row of tightly packed palisade parenchyma. Below the palisade are one or two layers of spongy parenchyma which line the adaxial surface and also the "inner cavity," if the latter is present. The epidermis of the adaxial leaf surface in contact with the stem, as well as that of the "inner cavity" in *Parastrephia lepidophylla* (FIG. 7) and *P. quadrangularis*, is thin and provided with only a thin layer of cuticle. The kinds and disposition of hairs vary from species to species. In *Parastrephia lepidophylla* (FIG. 7) a thick mass of uniseriate multicellular hairs lines the "inner cavity," but is found nowhere else; some multicellular glandular hairs are also found with the nonglandular hairs. In *P. quadrangularis* both the glandular and nonglandular hairs of the same type as in *P. lepidophylla* occur in the "inner cavity," but there is also a strong development of multicellular, multiseriate, stalked glandular hairs as well as of simple hairs, on the adaxial surface, forming a kind of "cement" between leaf and stem. In *P. teretiuscula* (FIGS. 14, 21) there is a complete reversal, with glandular and nonglandular hairs both occurring on the abaxial surface and none on the adaxial surface. Leaves of *Lepidophyllum cupressiforme* are largely devoid of trichomes, and only a few hairs are found on the adaxial surface. It should be mentioned that the leaves of *Parastrephia phyliciformis* (FIG. 15), considered under Type A, are somewhat intermediate between Types A and B.

TYPE C. This category is similar to Type A, but shows a marked simplification. The leaves are horizontally arranged and are generally a little larger, ranging from 10 to 50 mm. in length and from 2 to 10 mm. in width. Five species may be classed here: *Chiliotrichium diffusum*, *Nardophyllum lanatum*, *N. genistoides*, *Chiliotrichiopsis Keidelii*, and *C. ledifolia*.

The midvein region protrudes abaxially (as in Type A) and the leaf margins are revolute. However, since the margins are much less inrolled than in Types A and B and there is a greater horizontal development of the lamina, no so-called "inner cavity" is produced.

The adaxial leaf surface is provided with a thick epidermis, although not so thick as in *Parastrephia lucida* of Type A; neither is the cuticle as thick as in Types A or B. Below the epidermis there is usually one

FIGS. 13–19. Cross sections of leaves to show general outlines. 13, *Parastrephia lucida* (*Venturi 4750*, GH), × ca. 22; 14, *Parastrephia teretiascula* (*Cárdenas 86*, GH), × ca. 50; 15, *Parastrephia phyliciformis* (*Cabrera 7816*, LP), × ca. 45; 16, *Chiliotrichiopsis Keidelii* (*Fabris & Marchioni 1748*, LP), × ca. 15; 17, *Chiliotrichium diffusum* (*Eyerdam, Beetle & Grondona*, GH), × ca. 20; 18, *Parastrephia quadrangularis* (*West 6088*, GH), young leaf, × ca. 50; 19, *Chiliotrichium diffusum* (*Eyerdam, Beetle & Grondona 24098*, GH), × ca. 20 — compare with FIG. 17 from the same collection.

layer of palisade parenchyma succeeded by one or two layers of spongy parenchyma. The lower epidermis is thin and has a thin cuticle. In all species, the abaxial surface has a thick cap of uniseriate multicellular hairs. *Nardophyllum lanatum* (FIG. 8) has hairs also on the upper leaf surface, but not so profusely as on the lower. The glandular trichomes differ from species to species. In *Chiliotrichium diffusum* (FIGS. 12, 17, 19) they are numerous and restricted to the upper surface, where they are

embedded in small depressions. In *Nardophyllum lanatum* they are scarce and confined to the adaxial surface. The glandular hairs of *N. genistoides* are peculiar: they are usually uniseriate, consisting of a long stalk (formed by two elongated cells) and a round multicellular head; they extend in rows up to 2 mm. long on the margins and the upper surface. In *Chiliotrichiopsis Keidelii* (FIGS. 6, 16) and *C. ledifolia* the glandular hairs are of the common uni- or biseriate, multicellular type already described; they are on the lower surface only in the former species, and on both surfaces in the latter.

Aside from the glandular-hair differences, there are minor variations from species to species in the extent of inrolling of the margins, shape and size of the midvein, and lateral expanse of the blade. *Nardophyllum genistoides* is of special interest. Here the midvein region scarcely protrudes and the margins are only slightly bent. These conditions are very similar to those found in the following type, but there are some important structural differences.

TYPE D. Three species in two genera are treated here: *Aylacophora deserticola, Chiliophyllum densifolium*, and *C. fuegianum*. The leaves are small, 3–10 mm. long and 1–3 mm. wide, and linear to oblanceolate. They are thickish in texture and are covered both adaxially and abaxially by an equally thick epidermal layer and a cuticle. A layer of palisade parenchyma lies below the epidermis, which envelopes the leaves on both sides; in the middle of the lamina are one to three layers of spongy parenchyma interspersed with the vascular bundles. *Aylacophora deserticola* (FIG. 10) and *Chiliophyllum fuegianum* are hairy on both surfaces; in *C. densifolium* hairs are completely absent. All three species have glandular hairs on both leaf surfaces. The leaf margins are straight or slightly curved in *C. fuegianum*, the midvein region protrudes only slightly if at all and no "inner cavity" is found.

Vascular bundles. The vascular bundles of all species investigated are normal collateral bundles. All species of *Parastrephia* have an adaxially extended bundle-sheath associated with the midvein, enveloping a duct that is probably a resin canal (FIGS. 18, 20, 27). In *P. lucida* this duct is small, but in all other species it is very large and conspicuous. Except in *P. quadrangularis*, no resin canals were observed in primary stems. Species of *Parastrephia* and *Lepidophyllum* lack fibers in association with the vascular bundles. All other genera studied showed some xylary fibers, usually situated at each end of the bundle, or sometimes also between phloem and xylem, or even dispersed between the conducting elements themselves. The midvein of *Chiliotrichiopsis ledifolia* is surrounded by a bundle-sheath formed by one row of extremely large cells of about the same diameter as the radius of the bundle.

THE SHOOT

The primary stems are terete or slightly angled in transection except in species of *Nardophyllum* or *Aylacophora*. In all other genera the thick

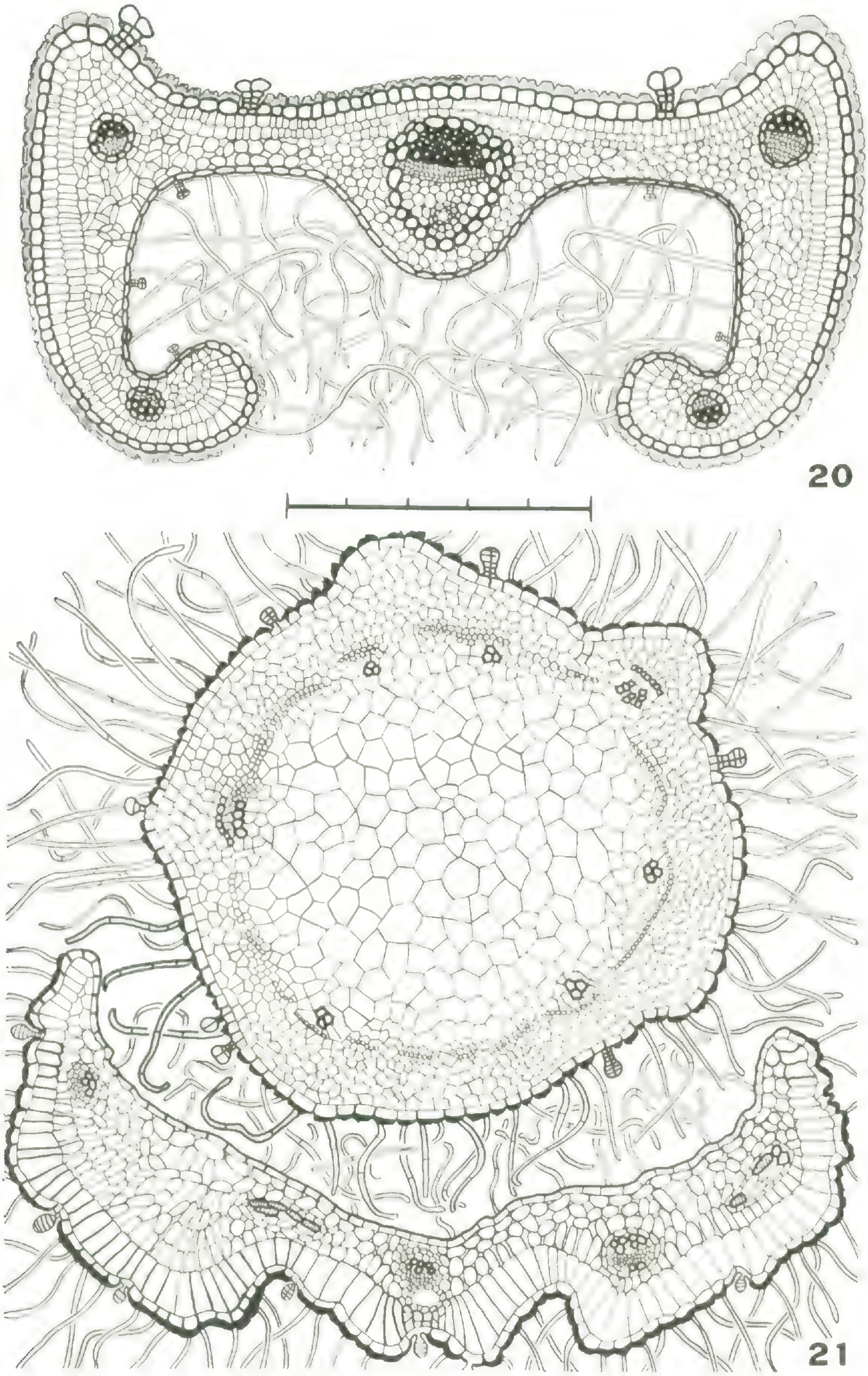

FIG. 20. Camera lucida drawing of cross section of leaf of *Parastrephia lucida* (*Venturi 4750*, GH), showing anatomical detail; hairs drawn schematically.

epidermis usually is covered by a thick layer of glandular and nonglandular hairs like those present in the leaves (FIGS. 21 & 23). The cortex is composed of thin, isodiametric cells, and occupies one-third to one-fourth of the diameter of the stem, surrounding a cylinder of collateral bundles. The pith consists of large, thin-walled cells at the center and smaller, thin- or sometimes thick-walled, fiber-like cells on the periphery. In *Parastrephia phyliciformis* the pith is unusually large, occupying over three-quarters of the diameter of the stem.

In all species of *Nardophyllum* the stem is angled or ribbed in transection. The epidermis, cortex, conducting tissues, and pith are similar to those just described. In addition, well-developed strands of sclerenchyma fibers along the ribs add rigidity to the stems. The pith in *Nardophyllum* is also sclerified, especially in *N. armatum*. In *N. bracteolatum* (FIG. 24) and *Aylacophora deserticola* (FIG. 22), deep grooves, reminiscent of the "inner cavity" of the leaf, and also lined with a thick cap of hairs, occur between the ribs. The epidermis is thick and heavily cutinized on the blunt, exposed surface of the ribs, but is thin and only slightly cutinized at the inside of the grooves, where stomata are present. The ribs are abundantly sclerenchymatous peripherally, while the grooves are lined with photosynthetic cortical parenchyma. It is clear that the primary shoots in these species are specialized for photosynthetic activity. In *Aylacophora deserticola*, in which the leaves are few and short-lived, photosynthesis must take place chiefly in the stem.

Nodal anatomy. The number of traces and gaps at the node has been considered to be a character of possible evolutionary significance, especially in woody plants, and may sometimes provide useful taxonomic information. In Compositae, the basic type of node is trilacunar with three traces; this type is basic also for most of the species studied here. Since type of node is usually very consistent in related groups — whole genera and sometimes even whole families — it is interesting to note that in eight of the species studied the node is unilacunar with a single trace, presumably by reduction. Unilacunar nodes have been reported previously in Compositae only for upper leaves in certain genera of Madineae (Carlquist, 1959). Even more remarkable, however, is the occurrence in *Parastrephia*, *Nardophyllum*, and *Chiliotrichium* of species with a trilacunar node and others with a unilacunar node.

Parastrephia phyliciformis, *P. lucida*, and *P. quadrangularis* have a trilacunar node; *P. lepidophylla* and *P. teretiuscula* are unilacunar. *Lepidophyllum cupressiforme* has a unilacunar node with one trace subtending each of the opposite leaves. *Nardophyllum armatum*, *N. genistoides*, *N. bracteolatum*, and *N. chiliotrichioides* all have a trilacunar node with three traces; *N. bryoides* and *N. obtusifolium* are unilacunar with a single trace. *Aylacophora deserticola*, *Chiliotrichiopsis Keidelii*, and *C. ledifolia* have

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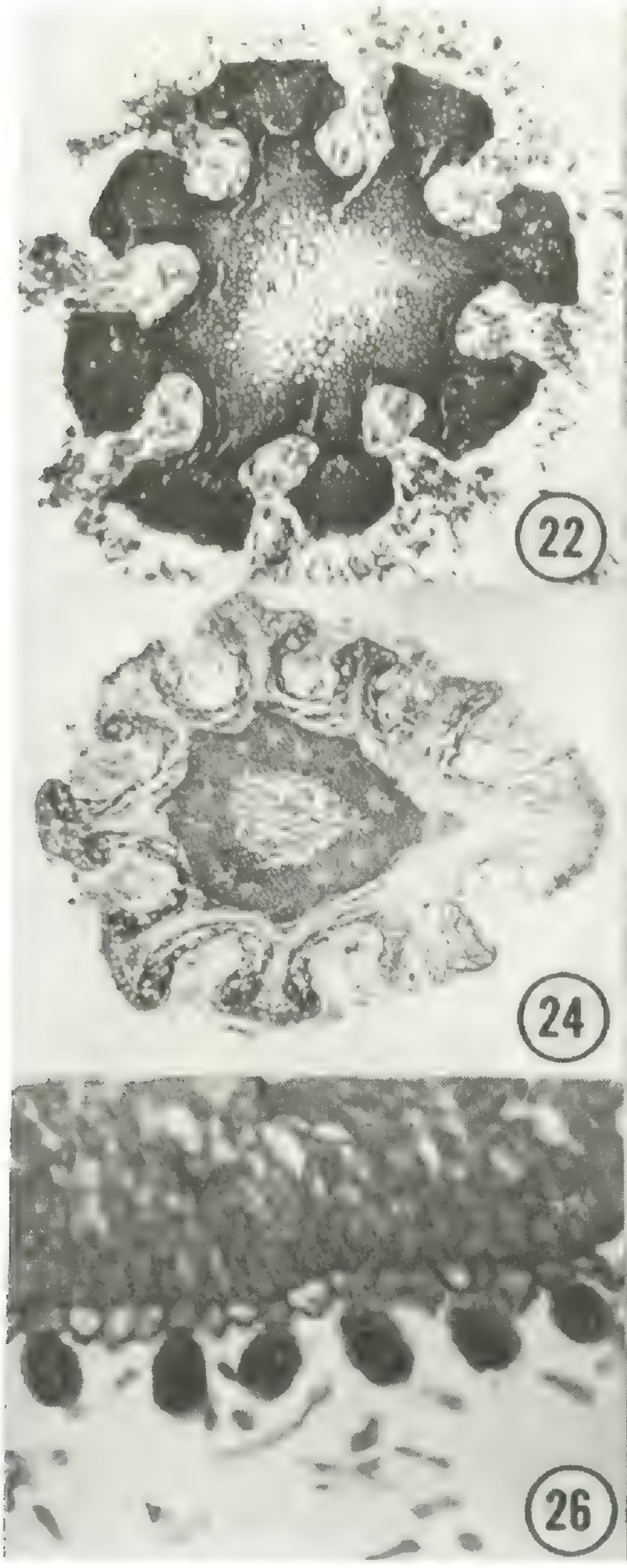
FIG. 21. Camera lucida drawing of stem and leaf cross section of *Parastrephia teretiuscula* (*Cárdenas 86*, GH), showing cellular detail. Each division of scale equals 0.1 mm.



FIGS. 22–24. Stem cross sections. 22, *Aylacophora deserticola* (*Cabrera 11053*, LP), × ca. 15; 23, *Parastrephia teretiuscula* (*Cárdenas 86*, GH), × ca. 20; 24, *Nardophyllum bracteolatum* (*Ruiz Leal 7212*, LP), × ca. 15. FIGS. 25–27. Details of leaves of *Nardophyllum bryoides* (*Eyerdam, Beetle & Grondona 24083*, GH). 25, Primordia in different stages of development, × ca. 50; 26, detail of glandular hairs, × ca. 100; 27, detail of leaf showing glandular hairs and resin canal, × ca. 75.

the trilacunar node common to the family. *Chiliotrichium rosmarinifolium* also has a trilacunar node, but that of *C. diffusum* is unilacunar. Finally, both *Chiliophyllum densifolium* and *C. fuegianum* have a unilacunar node with a single trace.

DISCUSSION

In the preceding paragraphs anatomical characters of leaf and node have been described. Their significance from the point of view of adaptation, evolution, and taxonomy remains to be seen. Cushion and mat plants have been the object of intensive investigations in the past, especially studies of an ecological or anatomical nature. An attempt to review the extensive literature is not pertinent to the present study and therefore only some salient information will be pointed out.

Hauri and Schröter (1914, p. 619) defined cushion plants as "perennials, herbaceous or woody, usually green chamaephytes, of spheric, hemispheric, or shingle-like, compact growth. The branches are numerous, with short internodes, covered more or less to the base and without interruption by small, more or less rigid, sessile leaves, withered in various ways. The branches end on the same level and are either closely appressed or the intervening cavities are filled by foreign material. In this manner is produced a certain strength, compactness, and closeness of the individuals, which consist of a living, appressed cover over a spongy mass of decaying material created by the plant itself" (free translation). If we adhere to this definition, none of the species studied can be considered cushion plants. However, Hauri and Schröter also recognized the existence of forms which do not fit their definition but which are nevertheless usually referred to as cushion or cushion-like plants. For these "cushion-like" types they proposed nine different categories. The plants studied here would come under the grouping of "spherical-shrubs" (*Kugelsträucher*), characterized by the loose growth (for cushion plants) of the branches, allowing the passage of air and light into the interior of the plants. In a later study, Hauri (1916) investigated the anatomical structure of leaves and stems of 73 species in 29 genera and 16 families. It is interesting to note that he found a strong convergence in anatomical characters: sessile leaves; a thick epidermis and usually a thick cuticle, or a thick layer of hairs, or both; a well-developed palisade layer; and a relatively slight sclerification of the stem. In this last respect, *Nardophyllum* and *Aylacophora*, of the seven genera investigated, do not agree.

Rauh (1939) presented a very thorough and complete analysis of cushion plants from a morphological point of view. According to him, cushion plants can be defined as "perennial, evergreen plants, with no well-defined central axis and numerous radial, stratified branches, the ends of which form a more or less compact surface due to a similar amount of growth in length" (free translation, p. 269). He divided the "growth-form system of cushion-plants" into seven main types: I. True cushion plants; II. Creeping cushions; III. Turf cushions; IV. Rosette cushions; V. Succulent cushions; VI. Cushion mosses; VII. Monocarpic ("hapaxanthe") cushion plants, that is, annual or biennial forms. He further subdivided these into subtypes. Type I, true cushion plants, was divided into high (radial-high) cushion plants and flat (radial-flat) cushion plants; the first subtype is further subdivided into cushion trees, spheric shrubs,

and hollow cushions. The species studied in the present investigation all fall under the category of spheric shrubs.

Although Rauh did not undertake any anatomical study, he reviewed the different leaf forms of cushion plants and grouped them into different types. Even if a detailed analysis of this classification is not in order here, a few comments may be made about his curved-leaf (*Rollblätter*) type. He characterized it as that in which the lamina, instead of flattening out at maturity, maintains the position it had in the bud. He indicated further that leaves with revolute margins are found only in *Frankenia* and *Anthobryum*, among cushion plants. As can be seen from the present study, revolute margins are more frequent among cushion-like plants (cf. also Cabrera, 1951; Carlquist, 1958). Although, on superficial inspection, the small leaves and inrolled margins might appear to be persistent juvenile forms, this view cannot be supported if the specialized anatomical structure of the leaf is taken into account. Likewise, the contention that sessile leaves in *Anthobryum* are the result of "arrested growth" in the petiole of a related and ancestral *Frankenia* must be discarded. A final word might be added with regard to Rauh's classification of the leaf types in cushion plants. Although a classification of leaf types can be helpful, a formal and complicated subdivision based exclusively on morphological types, regardless of phylogenetic origin, is not conducive to better understanding. When related species, sometimes even of the same genus, have to be separated to fit the classification, it does nothing to clarify taxonomic relationships. Rauh's proposed body types of cushion plants also suffer from the same defect.

Espinosa (1932) made a very careful and complete study of high-montane plants from the Cordillera de los Andes, especially the *páramos* of Ecuador. He recognized four main vegetative types: cushion plants, rosettes, bushes, and spiny bushes (*Dornsträucher*). Rosettes, cushion plants, and shrubs are commonest in the *puna* and *páramos*, spiny shrubs in the deserts of northern Chile and southern Perú, although they are fairly common also in the *puna* and in the "dry *puna*." Of more interest here are his anatomical investigations. He found that high-cordilleran plants generally are protected against desiccation by a thick epidermis and cuticle and a thick layer of hairs. Although none of the species studied by Espinosa shows leaves with the same cross section as those studied here, species with involute- and revolute-margined leaves were found, and also plants with leaves appressed to the stem, and some with large interior air chambers. Similar air chambers were reported for different species of the subantarctic islands of New Zealand by Cockayne (1909). No data on nodal anatomy were presented by Espinosa.

By way of summary, although none of the species studied by me can be considered a "typical" cushion plant, there seems to be general agreement that my material belongs ecologically to a cushion-like category. Some of the foliar features, such as thick epidermis, thick cuticle and compact palisade, appear to be relatively common among both cushion plants and cushion-like plants. On the other hand, the peculiar revolute-

margined leaf of some species of *Parastrephia* and *Nardophyllum* is less common and is only indirectly associated with a cushion habit. This type of leaf is widespread in Ericaceae (Hagerup, 1953), where it is frequently associated with dry habitats, but it is not very common outside that family.

Hagerup (1953), in reviewing the leaves of Ericaceae, considered the revolute projections to be not the true margins of the lamina, but a later outgrowth. This view was challenged by Hara (1956) on ontogenetic grounds. My own observations on shoot apices and primordia appear to confirm Hara's views, although they were not always decisive. Even at very early stages the primordia show configurations correlated with the final shape of the leaf (Fig. 25), and, although there is an increase in size of the revolute projections, they can hardly be interpreted as a "later outgrowth." The point is, in any case, a rather academic one, which depends largely on the particular definition of leaf margin.

Leaf venation in cushion plants has been studied very little. From my study of *Raoulia* (Solbrig, 1960), a New Zeland genus of true cushion plants, it would appear that a strong reduction in leaf venation may accompany the cushion habit in this genus. A similar conclusion is reached in the present study.

Nodal structure in cushion plants has also been neglected. The presence of two nodal types in the same genus is remarkable, and suggests greater flexibility in this character than has usually been assumed. The correlation with other structures suggests that in these Compositae the unilacunar condition is derived, adding to the body of evidence presented by Bailey (1956) that this is a common situation in advanced families of Angiosperms. That the trilacunar situation is always the primitive condition in Compositae cannot be said with certainty.

Although cushion plants are found in most high-montane areas of the world, they are most abundant in certain portions of the Andes of South America, especially the *páramos* of Colombia and Ecuador and the *puna* from Perú southwards, and in Patagonia (Andine Dominion of Cabrera, 1953). In these areas are found about 50 per cent of the pulvinate species known (Hauri and Schröter, 1914). Hauri and Schröter recorded 34 families and 78 genera containing a total of 338 species of cushion plants. Rauh (1939) put the number at about 400 species. Families with the largest number, according to these authors, are Compositae (15 genera, 52 species), Caryophyllaceae (12 genera, 49 species), Umbelliferae (4 genera, 34 species), and Cruciferae (2 genera, 34 species). The independent acquisition of this habit by more than 300 species of so many different families in different parts of the world suggests that this form of growth has some adaptive advantage, and this has been generally assumed. On the other hand, it is not very clear what the exact adaptation might be. The early interpretation was that cushion plants were xerophytic. When it was discovered that they often grow in moist habitats, the concept of "physiological xeromorphy" was developed (Hauri and Schröter, 1914; Hauri, 1917). Experiments by Walter (1931) indicated

for cushion plants on Pikes Peak, Colorado, a low osmotic pressure which discredited the idea of "physiological xeromorphy." Rauh (1939) presented a lengthy discussion of the subject. It suffices to say that different factors probably are operative, and that, although there is undoubtedly a convergence in morphological characteristics, there is no necessity to assume an equal convergence in the physiological responses of the plants. Only careful experiments on a larger number of plants could elucidate this problem. It is also quite clear that the plants show definite local adaptations within the broad environmental limits where they occur. All species considered in the present investigation grow in dry to very dry environments (Cabrera, 1958; Dusén, 1905; Fries, 1907; Skottsberg, 1916; Soriano, 1948), although such species as *Chiliotrichium diffusum* are found also in moister environments (Skottsberg, 1916).

A few words should be said about the possible taxonomic implications of the present work. Cabrera (1954) has considered the relationships of *Nardophyllum* and concluded that it is closely related on the one hand to the South African genus *Pteronia* L., and to *Chiliotrichium* and *Parastrephia* on the other. *Nardophyllum* differs from *Parastrephia* and *Chiliotrichium*, as well as from *Lepidophyllum*, *Chiliophyllum*, and *Chiliotrichiopsis*, by its tubular heads with all flowers perfect, the other genera having ovulate ray flowers, which can be either ligulate or tubular. Anatomically, *Nardophyllum* is separated from the genera mentioned by the possession of cortical sclerenchyma. It shares the tubular head and cortical sclerenchyma with the genus *Aylacophora*; the two genera differ in pappus and shape of achenes, characters which are generally variable within the tribe. There is also remarkable similarity in stem structure between *Aylacophora deserticola* and *Nardophyllum bracteolatum*; the leaf structure, on the other hand, is quite different in *Aylacophora* and *Nardophyllum*. In any case, it seems safe to assume that *Aylacophora deserticola* is closely related to *Nardophyllum*.

Cabrera (1954) separated *Lepidophyllum* and *Parastrephia* because of the opposite leaves, well-developed ray ligules, shortly papillose or glabrous achenes and paleaceous pappus of *Lepidophyllum*, contrasted with the alternate leaves, tubular or shortly ligulate ray flowers, hairy achenes, and bristly pappus of *Parastrephia*. Anatomically, *Lepidophyllum* is similar to *Parastrephia teretiuscula*, the main differences relating to the opposite leaves of the former. It seems likely that the similarities are due to convergence in these two reduced species.

Chiliophyllum and *Chiliotrichiopsis* differ in pappus and achenes: hairy pappus and weakly pubescent achenes in *Chiliophyllum* versus scaly pappus and strongly pubescent achenes in *Chiliotrichiopsis* (Cabrera, 1954). Anatomically, *Chiliophyllum* has a unilacunar node, *Chiliotrichiopsis*, a trilacunar node. This character is difficult to evaluate taxonomically in this group of genera since in *Nardophyllum*, *Parastrephia*, and *Chiliotrichium*, both unilacunar and trilacunar nodes occur in the same genus. The leaves of *Chiliophyllum* are less well developed than those of *Chiliotrichiopsis*.

The flowers of *Chiliophyllum* are also very similar to those of *Chiliotrichium*, the only difference being the color of the ligulate flowers, which are yellow in *Chiliophyllum*, but white in *Chiliotrichium* (Cabrera, 1954). In view of the situation in other genera of the tribe (Keck, 1958) this is a poor distinction. Anatomically there is not much difference, aside from the fact that one species of *Chiliotrichium*, *C. rosmarinifolium* has a trilacunar node.

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A REVISION OF THE ASIATIC GENUS LINOSTOMA (THYMELAEACEAE)

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The subtribe Linostomatinae of the Thymelaeaceae is composed of three closely related genera which have been combined taxonomically in various ways in the past. Previous treatments of these genera have not been inclusive, and, therefore, a preliminary survey to establish generic limits has resulted in considerable realignment of the species. Two of the genera, *Linostoma* Wall. ex Endl. and *Enkleia* Griff., are restricted to the area from India to Indochina, Malay Peninsula, and adjacent islands, while the third, *Lophostoma* Meissn., is restricted to the Amazon basin. Numerous examples of a disjunction between southeastern Asiatic and southeastern North American groups have been studied and reported but an Asian–Amazonian disjunction is unusual. For this reason an attempt will be made to define as precisely as possible the interrelationships of *Linostoma*, *Enkleia* and *Lophostoma*. In order to pursue these interrelationships it is believed essential to revise each of the genera concerned prior to generalizing about the subtribe as a whole. Accordingly, this revision of *Linostoma* is the first of a contemplated series.

SPECIAL MORPHOLOGY

Some of the more interesting morphological features found within the genus *Linostoma* during the course of this taxonomic investigation are presented in the following discussion. A few of these features have not been reported previously for the genus, and others are emphasized to indicate problems requiring additional investigation. Also included are several anatomical elements which have been employed previously as taxonomic characters and which I feel demand at least a summary review. Finally, additional information can be found in the body of the descriptions and in the discussion following each species.

It must be stressed that the number of specimens examined (indeed available) was far too few to obtain any but the very roughest type of information. A more thorough investigation which would include a study of the variation in individual plants in the field and under experimental conditions is necessary as the first step to an understanding of the variation exemplified in the herbarium specimens. However, even this brief study gives minor support to the taxonomic delimitations presented in this revision.

The leaves and flowers were prepared for study by gentle heating in water plus a commercial detergent until softened and then were cleared with a 5% solution of sodium hydroxide (Foster, 1950). The hydroxide

treatment often left the specimens in a too softened condition. This was remedied by treatment with chloral hydrate, which tends to harden the tissue and at the same time accounts for some additional clearing. In practically all instances it was necessary to bleach the specimens in 50% "Clorox" to obtain final clarity. The time necessary for the clearing processes varied widely from specimen to specimen.

The cleared leaves were stained with a 1% safranin solution in 95% ethyl alcohol for venation studies or with 5% ferric chloride and tannic acid in 70% ethyl alcohol for the study of cell types. The latter staining was particularly useful in studying the stomata. All specimens were dehydrated appropriately and mounted in Gum Damar or "Diaphane." As in the clearing processes, the staining times varied quite widely.

Cleared flowers were studied both unstained and stained; when stained, a 1% solution of safranin in 95% ethyl alcohol was used. I personally feel that the stained specimens are more useful, particularly when the finer vascularization is being studied. The stained flowers were dehydrated and mounted in Gum Damar.

Leaf cross sections and petioles were prepared for study by boiling in water or by clearing as in the procedure outlined above. They were embedded in paraffin through a tertiary butyl alcohol series and sectioned. A safranin-fast green staining schedule was followed.

In addition, free-hand sections stained with potassium iodide and sulphuric acid, as well as with phloroglucin and hydrochloric acid (Foster 1950) were later found to be useful in determining the degree of lignification of certain tissues. This technique has been employed with stems, petioles, leaves and bracts.

Vegetative Morphology. The vegetative axis is monopodial, but the precocious development of axillary buds often obscures this nature. Several types of branching usually can be observed within any single relatively large collection. The simplest pattern is one in which dichotomous branching, with equal development of both axes, appears to have taken place. This type is the result of the destruction of the apical bud followed by development of the opposite axillary buds. An aborted terminal bud often may be observed in the fork of the dichotomy but it is gradually obscured with time. A second type of branching, also appearing to be dichotomous but unequally so, is the result of the continued growth of the main axis accompanied by the development of one of the axillary buds of the subtending node. The most striking pattern, however, is in the form of a trichotomy. This pattern is formed by the continued growth of the main axis accompanied by the simultaneous development of both axillary buds of the subtending node. The members of the trichotomy may be developed equally or unequally, and, in addition, the lateral axes may be slightly subopposite, depending on the exact position of the axillary buds.

In a few instances, the branching patterns described above are not clear-cut because the leaves subtending the developing axillary buds some-

times do not appear to be present. These leaves are then borne on the developing axillary branch beyond the point of external furcation. They are usually near the division and are unpaired, in contrast to the leaves of the normal axis. The trace which supplies these leaves is initiated below the external furcation as is the trace of the axillary bud. Immediately below the external furcation the division of leaf and axillary bud traces is not yet complete. For some unknown reason the leaf is then "carried out" onto the developing axillary branch which it actually subtends. This phenomenon is more prevalent in the inflorescence and is further discussed there.

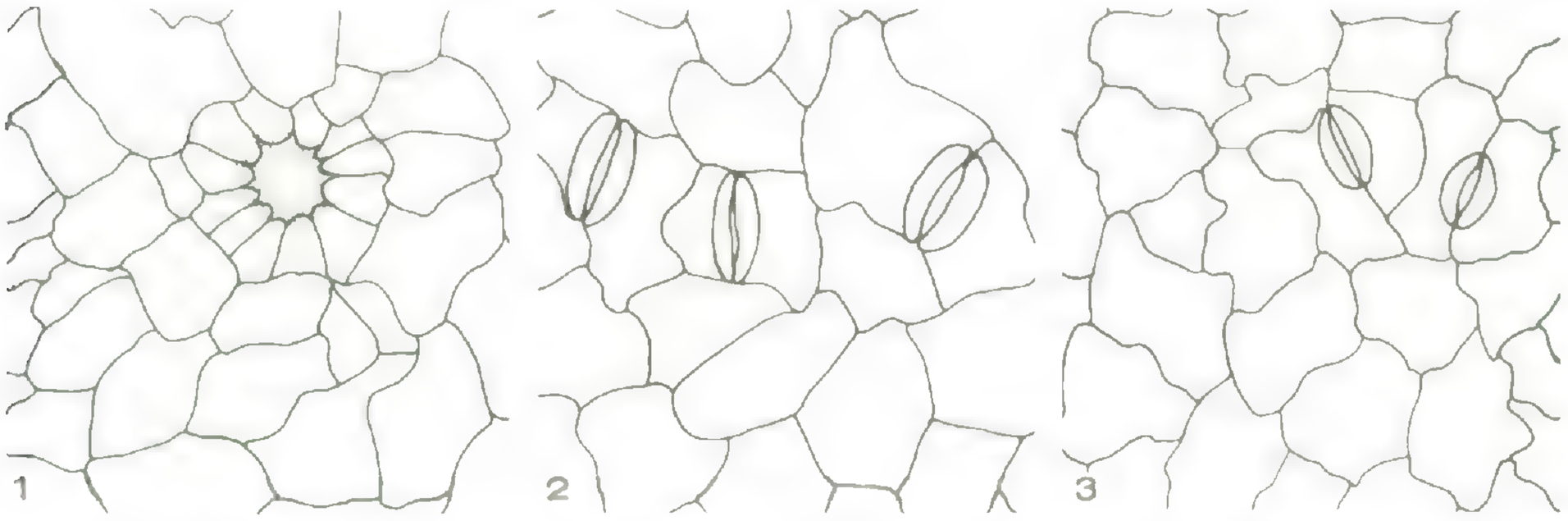
The axillary branches themselves are of interest in that they may be ascending or become weakly to strongly uncinate, facilitating climbing or scrambling. The "hooks" are similar in appearance to those found in species of *Cardiospermum* (Sapindaceae) or in *Schefflera caudatifolia* Merrill (Araliaceae). There are reports (Metcalfe & Chalk, 1950) based on stelar anomalies indicating the possible origin of genera with shrubby or treelike habits from lianalike ancestors. It is because of the development of the uncinate branches that the habit of individual species appears to be so diverse. I suspect that the plants of *Linostoma* are erect shrubs or trees which are not above scrambling if the opportunity presents itself.

The presence of an extraxylary fiber sheath surrounding the stele often is used as a diagnostic characteristic of the family. These fibers are often employed as twine in various parts of the world. They have relatively thick walls of cellulose and, in this genus, may become slightly lignified after a number of years. The lack of strong lignification of the fibers may contribute in part to the flexibility of the stems.

The structure of the leaf was investigated because of the widespread use of the venation pattern as a means of distinguishing between *Linostoma* and *Enkleia*. The leaves are dorsiventral. The upper epidermis, covered by a rather thick cuticle, is composed of relatively large tabular cells in *L. persimile* and *L. pauciflorum* and is devoid of stomata. A hypodermis of large, thin-walled cells is also found in these two species. In *L. decandrum* a single epidermal layer, comparable to the double layer of the other species, is found. The palisade layer immediately below is compact and composed of more or less isodiametric cells which are at most only a fifth the size of the epidermal cells. This palisade appears to be three or four cells thick. Within this layer or the one following, occur some large, thin-walled cells which contain druse-like crystals. These crystals are most prevalent in *L. decandrum*. The spongy parenchyma layer below the palisade is extremely loose, with very large air spaces. The cells composing this layer are comparatively large and generally are branched. The lower epidermis is composed of tabular cells which, in the case of *L. pauciflorum*, are conspicuously bullate on the outer periclinal wall. This peculiar papillation of the lower epidermis gives a characteristic farinose appearance to the lower leaf surface when viewed under low magnification. The cells of the lower epidermis, which is in-

terrupted by numerous stomata, are consistently smaller than those of the upper epidermis.

In *Linostoma persimile* and *L. pauciflorum* the stomata are similar, and it is impossible to distinguish these two species on the basis of stomatal type or size (TEXT FIG. I, *2*, *3*). These stomata are of the ranunculaceous type (accessory cells morphologically similar to the surrounding epidermal cells). This stomatal type has not been reported previously for the genus, although it is well known in other genera of the family. The guard cells are borne in the same plane as the epidermal cells.



TEXT FIG. I. Camera lucida drawings of the lower leaf epidermis of *Linostoma*. 1, *L. decandrum* (*Parry 410*); 2, *L. persimile* (*Garrett 1397*); 3, *L. pauciflorum* (*Kerr 11820A*). Stippling indicates stoma on different plane from surrounding cells.

The stomatal condition is more complex in *Linostoma decandrum*. Instead of a pair of accessory cells as in the previous species, there is a cluster of small cells completely surrounding the stoma. Each cell is awl-shaped and bends slightly over and beyond the guard cells so that an urceolate structure is formed. The guard cells are situated at the base of this pit and are, in addition, borne in a plane above that of the lower epidermis (TEXT FIG. I, *1*; also Solereder *Fig. 174, B, C* and repeated in Metcalfe and Chalk, *Fig. 284, B, E*).

The pinnate venation is essentially similar in all species of the genus. The primary lateral veins are very numerous and close to each other (several millimeters apart at most) and are more or less straight, parallel, and simple, but sometimes dichotomize. Each vein is subtended by an extraxylary fiber-sheath which is often more extensive than the vein which it supports. Each primary vein terminates in, and contributes to, a submarginal vein. The submarginal vein, with accompanying fibers, is often better developed than the contributing lateral veins (except in *L. persimile*). Its proximity to the margin varies slightly among the species.

The secondary veins, after departing from the primary veins, run more or less parallel to them. The very fine appearance of the venation is due to this parallel orientation of veins and veinlets. The veinlets are also subtended by the extraxylary fibers. These fibers react strongly with potassium iodide and sulphuric acid to give a deep blue color but do not give a color reaction to phloroglucin and hydrochloric acid. On this basis

it appears that they are composed of cellulose and are not lignified. The fiber sheath extends almost to the end of the veinlet where it is often replaced by variously shaped sclereids. In *Linostoma persimile* these sclereids do not extend to the vein-ending, but in both *L. decandrum* and *L. pauciflorum* they extend either to the vein-endings or slightly beyond them (see TEXT FIG. II).

Cross sections of the petiole were studied to check information in Metcalfe and Chalk (1950) indicating the presence of intraxylary phloem in petioles of *Lophostoma* and *Enkleia* but not *Linostoma*. In all species of *Linostoma* the xylem, at mid-petiole, is arc shaped and often is interrupted by rays a single cell broad. In *L. decandrum* and *L. pauciflorum* it appears that phloem can be found both above and below the xylem-arc, thus indicating the presence of intraxylary phloem within the genus, contrary to previous reports. In *L. persimile* the phloem is found only below the xylem-arc. At best this seems to be only an academic point and appears to lack taxonomic significance.

The fibers which usually accompany the vascular bundles either are poorly differentiated in the petioles or are lacking altogether. When present, they have a negative color reaction with phloroglucin and hydrochloric acid. However, they stain very dark blue with potassium iodide and sulphuric acid indicating the cellulosic nature of the cell walls.

Reproductive Morphology. At the time of the initiation of the flowering response the vegetative pattern in the terminal portion of the shoot becomes modified. The changes which take place in the external morphology of the shoot at this time possibly are controlled by the same physiological forces which cause the induction of the flowering response.

The same basic terminology which I applied to the inflorescence of *Daphnopsis* in a previous paper (1959, pp. 262, 263) is used here. The inflorescence is considered as being composed of the basic units of primary peduncle, rachis, secondary peduncles and flowers with their pedicels. There are a few additional features in the inflorescence of *Linostoma* not found in *Daphnopsis*, and these are discussed below.

The flowering shoot is composed of many inflorescences, the sum of which appears to form a single large and highly branched, terminal inflorescence. The flowering response destroys the apical dominance of the stem apex, and the axillary buds of several subtending nodes begin development. This complex change must take place during the initiation of the affected parts and prior to their subsequent elongation. The resulting precocious development of the axillary branches is responsible for the decidedly peculiar appearance of the inflorescence. The main stem axis appears to trifurcate (see also discussion of branching patterns) without good cause, i.e., without subtending leaves. This pattern is due to the initiation of the leaf traces and the axillary bud traces shortly below the external furcation, followed by rapid elongation to the extent that the leaf is "carried out" onto the axillary shoot which it actually subtends. The external relationships of vegetative shoot, axillary branches and

leaves are obscured. The developing axillary shoots may undergo several such divisions until a large paniculiform structure is developed. As a result, the primary peduncle often bears near its base the reduced, displaced leaf of the subtending node. This displaced leaf is homologous to the bract found on the compound inflorescences of some species of *Daphnopsis* (especially *D. americana*).

At the apex of the primary peduncle is borne a single small bracteole, which is usually caducous but occasionally persistent. This structure is further discussed following *L. pauciflorum*.

In addition, the primary peduncle bears a pair of bracts. These bracts are opposite to alternate and are borne at or below the middle of the primary peduncle (*Linostoma decandrum* and *L. persimile*), or from the middle to the summit (*L. pauciflorum*). These bracts appear to be expanded fully, or nearly so, by the time the flowers attain anthesis. This contrasts with the situation in *Enkleia* in which the expansion of bracts is delayed until shortly after anthesis. The function of these bracts is uncertain, although Domke has used the very appropriate term "Flugbrakteen" to describe them and Ridley has included this genus in his book (1930) on plant dispersal under the heading "Bract Wings." Speaking of the bracts in *Linostoma* he says (p. 92), "They become pale and papery when the fruit is ripe, and are detached, adhering to the fruit, so as to be blown away separately." He attributes the small size of the plants of *L. persimile* to the drupe being too heavy to be borne away by the bracts, whereas, in *L. decandrum* and *L. pauciflorum* the drupe is light enough to be easily drifted. Finally, he says (p. 93) "Here the reduction of the number of fruit produced on the spray, and the persistence of the terminal pair of leaves, has converted a bird-dispersed plant into a wind-dispersed one, and has allowed the plant to be successful in climbing to the top of the forest." Theoretically, I disagree with Ridley because it appears, on the basis of herbarium material, that all separations of fruit plus peduncle with bracts are mechanical accidents. In these cases the peduncle at the point of separation is irregularly broken and does not seem to be as easily separated as at the articulation zone between pedicel and secondary peduncle. Ridley has seen the plants in nature and what appears to be theoretically improbable may occur in actuality.

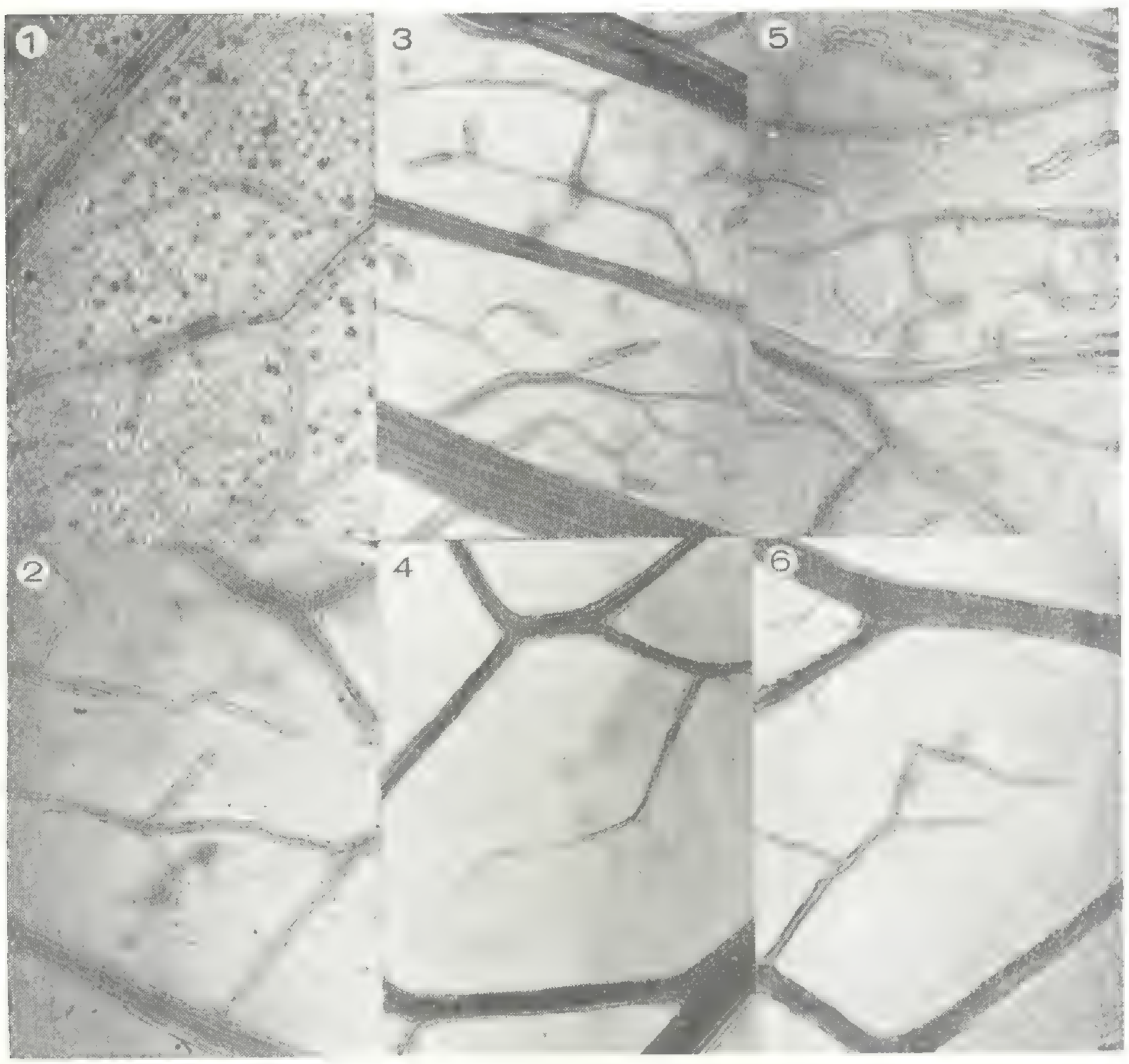
The shape and structure of the bracts are in several respects different from those of the foliage leaves. The bracts vary from ovate to oblanceolate but are of a shape and size usually quite dissimilar from that of the leaves. In addition, they are much thinner than the leaves and are distinguished further by their white to cream color. In spite of their extreme thinness, the bracts retain the same morphological components (i.e., epidermis, palisade and spongy parenchyma) and in approximately the same ratio as the leaves.

Another, and perhaps more striking, characteristic of the bracts is the relative spaciousness of the venation. The venation pattern is, in fact, more like that which one would expect to find in leaves, i.e., more reticulate. The number of primary veins is greatly reduced from the number

found in leaves. In addition, the number of secondary, and particularly smaller, veins is much lower. The lack of development of the smaller veins accounts for the appearance of spaciousness of the venation. As in the leaf, a submarginal vein is present in all species.

The extraxylary fiber sheath associated with the veins differs from that of the leaves in one striking aspect. In contrast to the leaf, the sheath supporting the minor veins is not constituted entirely of fibers but often has an outer layer composed of relatively short sclereids. These sclereids are irregularly shaped, with at least one surface noticeably enated. This characteristic allows microscopic identification of leaves and bracts (see TEXT FIG. II).

The fiber sheath reacts to the lignification and cellulosic tests in the same way as in the leaves. The color reaction indicating cellulosic walls lacking lignification is less intense than in the leaves. In like manner, the color reaction indicating lignified xylary elements also is much less



TEXT FIG. II. Photomicrographs of fine venation of leaves and bracts of *Linostoma*. 1. *L. decandrum*, leaf (*Wallich 4203*); 2. *L. decandrum*, bract (*Wallich 4203*); 3. *L. persimile*, leaf (*Garrett 1436*); 4. *L. persimile*, bract (*Garrett 1436*); 5. *L. pauciflorum*, leaf (*Hallier B.2261*); 6. *L. pauciflorum*, bract (*Hallier B.2261*). Note numerous crystals in leaf of *L. decandrum*.

intense, and it seems that the tissues of the bracts are developed much less than those of the mature leaves.

The flowers are arranged on the rachis in an indeterminate fashion (the lowermost flower blooming first). The flower clusters are umbelliform to subracemiform, depending on the relative length of the rachis. I suspect (without substantiating evidence) that the condensation of the rachis and the resulting clustering of flowers is due to selective pressures in favor of the formation of a pseudanthemum.

The flowers are bisexual, regular, pentamerous, perigynous, and pedicellate. They are probably conspicuous at anthesis by their coloration and by the presence of the light-colored subtending bracts.

The terminology applied to the parts of the thymelaeaceous flower has varied with the individual author's personal inclinations. Accordingly, I am retaining the same terminology that I used in *Daphnopsis* (Nevling, 1959) and that for the same reasons. Further gross morphological information, beyond that presented in the following discussion, concerning the flower may be found in the specific descriptions.

The calyx tube is appendicular in origin, that is, composed of the fused bases of calyx, corolla, and androecial members. It is always tubular, although the exact shape is variable, and surrounds the superior ovary. The exterior is glabrous, while the interior varies from entirely villous to glabrous. The trichomes are exclusively unicellular and unbranched.

The tube is vascularized by ten distinct veins which are marked externally by conspicuous ridges. Near the orifice the traces to the androecium depart, one to each stamen. Above the departure of androecial traces the vascular pattern becomes exceedingly obscure due to the proliferation of traces and to the overlying pubescence. I am not satisfied with my results in this critical area of the calyx tube.

The size and shape of the five calyx lobes vary among the species. The position of the lobes at anthesis is a more important taxonomic character. In *Linostoma decandrum* they are strongly reflexed, in *L. pauciflorum* they are spreading, and in *L. persimile* they are erect to slightly spreading. In all species the lobes are vascularized by three main veins. The lateral veins often proliferate at the orifice, and all send off numerous branches which often anastomose, particularly towards the lobe apex. Extraxylary fibers are present even on these small veins.

The ten petals are inserted in pairs at the orifice of the calyx tube in an alternisepalous position just above the outer staminal whorl. Two closely related petal types are found in the genus: (1) in *Linostoma decandrum* the clavate petals are united at their bases by an inconspicuous annulus; (2) in *L. pauciflorum* and *L. persimile* the clavate or liguliform petals are free at their bases. In all species the petals are glabrous and erect.

The shape of the petal apex has been found to be a useful taxonomic character. It is dependent on differential growth patterns (particularly differential elongation of separate whorls). The elongation patterns are reflected in the relative position of petals, anthers and stigma in the

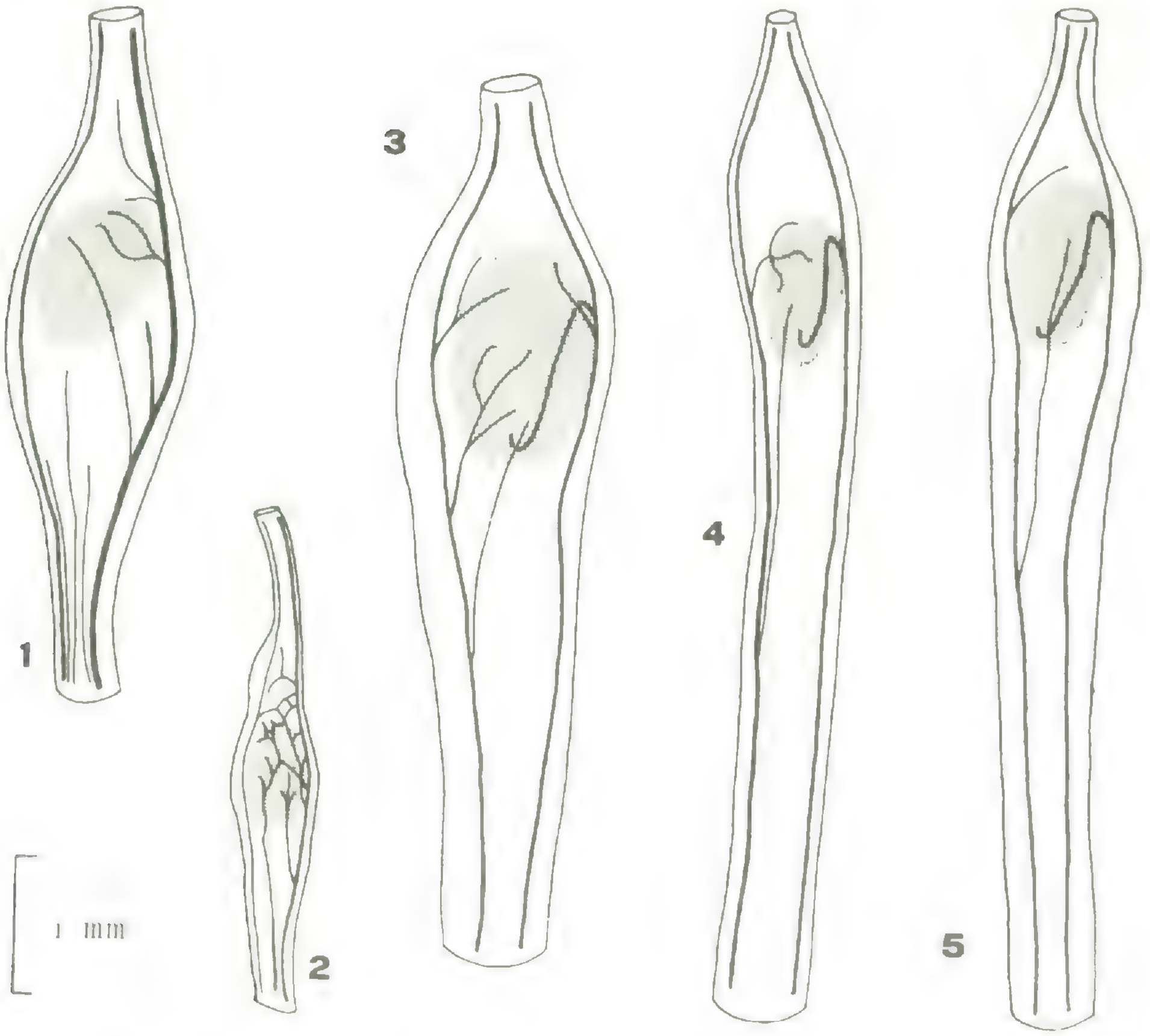
mature flower. In this respect two exsertion orders are found: (1) stigma, anthers and petals in *Linostoma decandrum* and *L. pauciflorum* (petal apex obtuse or irregular); (2) petals, stigma and anthers in *L. persimile* (petal apex acute).

The distortion of the petal apex in *Linostoma decandrum* occurs as the pairs of petals develop in the alternisepalous position. In the bud their apices become appressed to the base of the developing alternisepalous anther. Elongation of the petal apparently occurs at a slightly faster rate than that of the developing staminal filament, with the result that each petal apex clasps one of the lower lateral margins of the alternisepalous anther, thus deforming the petal apex. Although the filaments subsequently elongate and the petals undergo further elongation, the apices never recover from the initial contact with the anther. As a result, the petal apex is often cup-shaped or truncated with one lateral margin (that toward the calyx lobe) noticeably longer than the other. This same situation is found in *L. pauciflorum* to a much lesser degree, with the result that the petal apices are never as strikingly deformed as in *L. decandrum*. The acute petal apex of *L. persimile* is due to the lack of interference of petal elongation by the androecium. It is impossible to say whether this condition is advanced or primitive in relationship to that found in *L. decandrum* and *L. pauciflorum*.

In *Linostoma persimile* and *L. decandrum* vascular tissue is lacking in the petals. This is really quite surprising, for petal length in these species is 3.5 and 3.5–6 mm. respectively. It is difficult to understand why fleshy structures of this size require no vascularization. In *L. decandrum* the petals are inserted between the midrib supplying the calyx lobe and the lateral veins, which at this level have already divided several times. It does not appear to be associated more intimately with the lateral veins than with the midrib as might be expected.

The petals of *Linostoma pauciflorum* are vascularized by a single trace. I have observed an exception in one petal in which the trace divided near the base and two well-developed traces were formed. I have been unable to determine the connection of the petal trace with a calyx tube trace. The trace is usually 5–10 tracheids in diameter, and these tracheids have annular to helical thickenings. Toward the petal apex the tracheids become noticeably shorter and the trace finally ends blindly.

The androecium consists of ten stamens inserted on the calyx tube just below the petals. The stamens are inserted either in two whorls (*L. persimile* and *L. pauciflorum*) or in a single whorl (*L. decandrum*). The five stamens of the upper whorl are in the antisepalous position, while those of the lower whorl are alternisepalous. The single whorl of *L. decandrum* is in reality two closely intermeshed whorls, for the traces supplying the alternisepalous stamens depart from the lateral commissural calyx traces (in respect to the position of these in the calyx lobe) some distance below those of the antisepalous stamens. The traces supplying the antisepalous stamens are continuous with those of the median calyx traces.



TEXT FIG. III. Camera lucida drawings of vascularization of stipe and ovary of *Linostoma*. 1, *L. decandrum* (*Parkinson 316*); 2, *L. persimile* (*Garrett 1436*); 3–5, *L. pauciflorum* (*Ridley 1868*, *Hallier B.2261*, *Haviland 1759*). Stippled portion is the approximate area occupied by the ovule; all vascular bundles, with the exception of the hook-shaped ovular trace in figs. 3–5, are in the ovary wall; only the bundles in the ovary wall facing the viewer are represented.

The filaments are filiform, and those of the antisepalous stamens are usually longer than those of the alternisepalous ones. They are glabrous, except in a single anomalous flower in which they are hispid. Vascularization is by a single vascular bundle which either ends blindly somewhat below the connective tissue or enters only the lower half.

The anthers are exserted, except for those in the alternisepalous whorl of *Linostoma persimile*. They are 4-lobed and 4-loculed in cross section. Dehiscence is longitudinal. The connective is basally inflated in *L. pauciflorum*, and to a lesser degree in *L. decandrum*, so that the pollen sacs are displaced to its lateral margins. In *L. persimile* there is no basal inflation but the connective is produced beyond the pollen sacs.

The pollen of the three species is, for all practical purposes, uniform. It is polyporate and highly sculptured. The grains vary between 40 and 60 micra in diameter, and, although an insufficient number have been

measured, it appears that those of *Linostoma persimile* are the smallest and those of *L. pauciflorum* are the largest.

The disc is borne at the base of the calyx tube and closely surrounds the stipe supporting the ovary; in many previous descriptions the disc has been considered to be absent in the genus. It consists of irregular lobes which are free or connate and sometimes adnate to the calyx tube. The number of lobes is extremely variable within flowers of the same inflorescence and therefore is of little taxonomic consequence. Externally the disc appears fleshy and is glabrous, except in *Linostoma decandrum* in which it may support a few trichomes. Since I have had little success in clearing the disc, which scarcely attains 0.5 mm. in height, I have been unable to determine the vascularization, if any.

The gynoecium is composed of a single pistil, presumably of the pseudomonomeric type, i.e., one fertile and one sterile carpel. It is borne on a stipe (gynophore) which varies in length among the species. In the specific descriptions in the taxonomic treatment the length of stipe and ovary are combined because of the gradual transition between them.

The ovary is superior, ellipsoid to obovoid, and unilocular. It is usually densely sericeous, although occasionally sparsely so in *Linostoma pauciflorum*. The trichomes are unicellular, erect, and quite shiny (at least in herbarium specimens). The pattern of vascular supply to the ovary seems quite distinct among the species (see TEXT FIG. III). *Linostoma pauciflorum* is immediately distinguishable by the well-developed ovular trace (further discussed under the species), the presence of only two traces at the base of the stipe, and few lateral traces. *Linostoma persimile* can be distinguished from *L. decandrum* by the more reticulate secondary venation arising from the main veins. The apparent lack of an ovular trace in the last two mentioned species is curious and requires further investigation. In all species the single, anatropous, two-integumented ovule is semipendulous from the upper locule wall.

The style is borne terminally, although it sometimes appears to be eccentric, in which event the trichomes must be removed before its true position can be seen. It is filiform and is vascularized by two relatively large traces which stand opposite each other. The style is generally glabrous, except in a few specimens of *Linostoma pauciflorum* where a few trichomes can be found. The stigma is capitate or mammiform. (See also discussion following *L. persimile*.)

The flowers of all three species are pedicellate. The junction of pedicel and secondary peduncle is clearly marked by an articulation. In the area of articulation parenchyma cells may be formed at the expense of other tissues. A longitudinal section through the point of articulation in *Linostoma decandrum* has been figured by Leandri (*Fig. 23, 3,4.* 1930).

In general, the fruits are preserved very poorly and I do not feel qualified to comment upon them at this time. The longitudinally ruptured calyx tube is persistent in *Linostoma decandrum* and can be seen at the base of the fruit. In *L. persimile* and *L. pauciflorum* the calyx tube is accrescent and surrounds the fruit.

GEOGRAPHY

The three species have a composite range extending from India to Indochina, the Malay Peninsula, and the island of Borneo. The distribution is not complicated because of the small number of species. Distributions of the individual species have been plotted on MAP I, which is a part of one of Goode's Series of Base Maps published by the University of Chicago Press. The symbols indicate places of collection only and are in no way indicative of the relative frequency of the plants.

At the present time too little is known of the ecological situations in which the plants grow to give any rational discussion but in only one species, *Linostoma decandrum*, does the distribution appear to be unusual. The disjunction shown by this species is, in all probability, a real one with a lack of suitable habitats between the two areas. There seems to be no morphological basis for the erection of any infraspecific categories in this case.

MATERIALS

This revision is based on specimens from the following herbaria, the abbreviations for which are taken from Lanjouw & Stafleu, *Index Herbariorum*, Part I, Ed. 4 (Regnum Vegetabile 15. 1959).

A	Arnold Arboretum of Harvard University, Cambridge
BM	British Museum, London
C	Botanical Museum and Herbarium, Copenhagen
G	Conservatoire et Jardin botaniques, Genève
GH	Gray Herbarium of Harvard University, Cambridge
K	Herbarium, Royal Botanic Gardens, Kew
L	Rijksherbarium, Leiden
M	Botanische Staatssammlung, München
P	Muséum National d'Histoire Naturelle, Paris
U	Botanical Museum and Herbarium, Utrecht
US	U. S. National Museum, Smithsonian Institution, Washington
W	Naturhistorisches Museum, Wien

I wish to take this opportunity to thank the directors and curators of the above institutions for the many courtesies extended to me. This revision would not be possible without their co-operation. I also wish to thank my colleagues of the Arnold Arboretum and Gray Herbarium for helpful suggestions, technical assistance, and constant encouragement.

TAXONOMY

Linostoma Wall. ex Endl. Gen. 331. 1837 (TYPE: *L. decandrum* (Roxb.) Wall. ex Endl.).

Linostoma Wall. Cat. n. 4203. 1831, sine descript.

Linostoma sect. *Eulinostoma* Meissn. in Mart. Fl. Bras. **5**(1): 72. 1855 (TYPE: *L. decandrum* (Roxb.) Wall. ex. Endl.).

Linostoma subg. *Nectandra* Kurz, Jour. As. Soc. Bengal **39**(2): 83. 1870 (TYPE: *L. decandrum* (Roxb.) Wall. ex Endl.).

Trees, shrubs or lianas, often scrambling, the stem monopodial, although frequently dichotomizing or trichotomizing, the axillary branches sometimes modified for climbing, the bark containing many fibers, becoming rugose with drying. Leaves opposite (or sometimes approximate) to alternate, simple, pinnately veined, entire, petiolate, estipulate. Inflorescences borne from the terminal portions of young stems, subracemiform, umbelliform, or rarely the flowers solitary, the primary peduncle bearing a pair of bracts and a single bracteole. Flowers bisexual, pentamerous, perigynous; calyx tube urceolate, ellipsoid or tubular, nonarticulated, ribbed, red, yellow, greenish white or white, glabrous without, glabrous or variously pubescent within; calyx lobes 5, subequal, quincuncial, erect to reflexed at anthesis; petals 10, ligulate to clavate, sometimes with a minute annulus at the base, glabrous; stamens 10, inserted in 1 or 2 whorls, the upper whorl antisepalous, the lower whorl alternisepalous, the anthers filamented, basifixed, longitudinally dehiscent, the connective sometimes produced beyond the pollen sacs or inflated; disc of irregular lobes, sometimes basally connate, sometimes adnate to the calyx tube; gynoecium single, pseudomonomeric, superior, variously stipitate, unilocular with a single anatropous ovule, the style terminal, the stigma capitate or mammiform. Fruit drupaceous, the calyx tube sometimes persistent or accrescent.

KEY TO THE SPECIES

a. Leaves to 10 cm. long, thick-coriaceous, the apex acute, acuminate or subcaudate; inflorescences 3–12-flowered; calyx tube villous within; calyx lobes generally as long as or longer than the tube, strongly reflexed; calyx persistent but not accrescent in fruit. ..... 1. *L. decandrum*.

a. Leaves to 5 cm. long, thin-coriaceous, the apex mucronulate and acute, obtuse, truncate or retuse; inflorescences 1–6-flowered; calyx tube villous or glabrous within; calyx lobes at most half as long as the tube, erect or spreading; calyx accrescent in fruit.

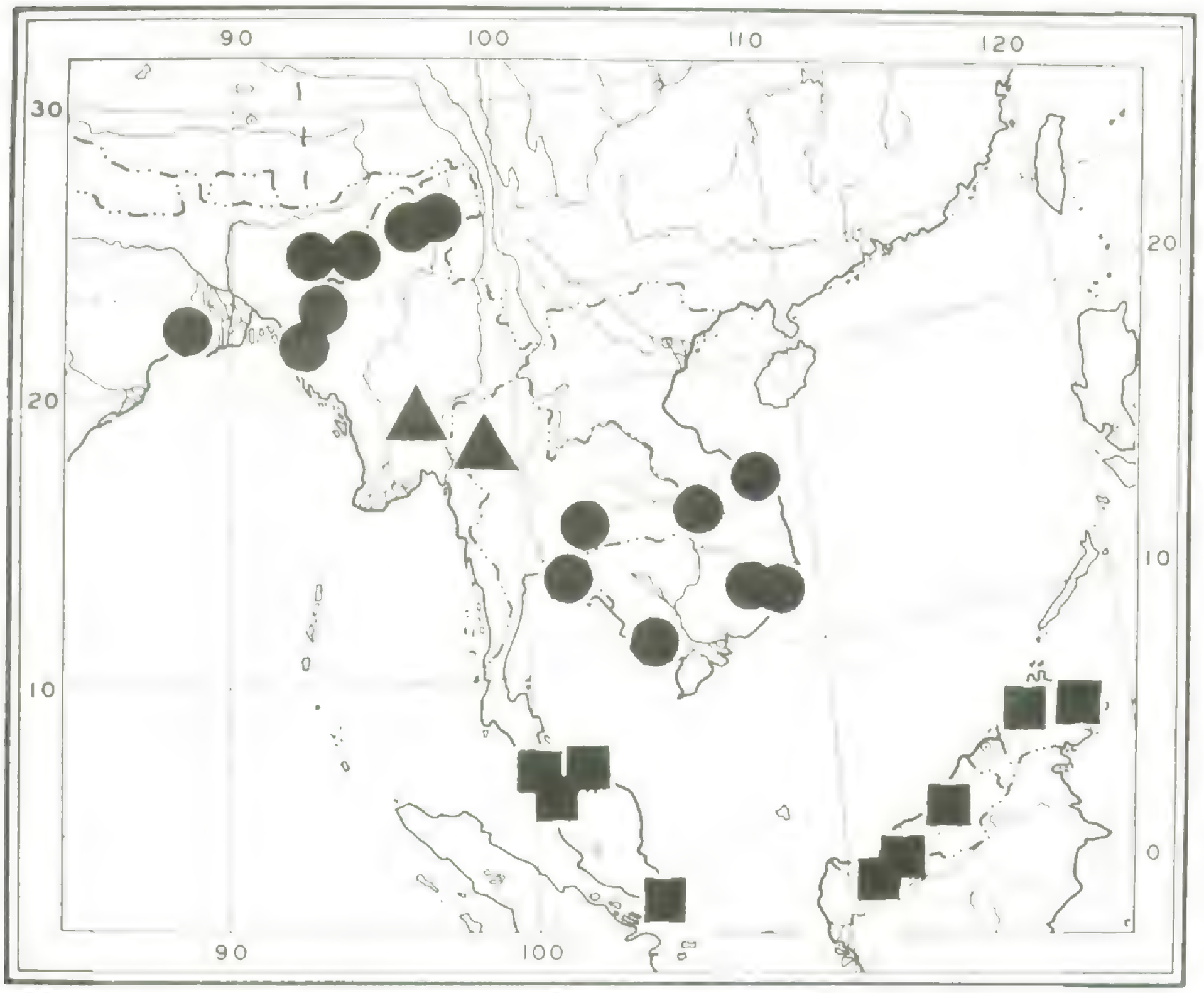
b. Bracts subopposite, borne at the middle of the primary peduncle or below; calyx lobes erect; petals exserted beyond the stigma and anthers; connective produced beyond the pollen sacs but never inflated; style 6–7.5 mm. long. ..... 2. *L. persimile*.

b. Bracts opposite to alternate, at least one of the pair borne near the summit of the primary peduncle; calyx lobes spreading; stigma and anthers exserted beyond the petals; connective inflated so as to separate the pollen sacs at least basally but never produced beyond the pollen sacs; style 6–20 mm. long. ..... 3. *L. pauciflorum*.

1. Linostoma decandrum (Roxb.) Wall. ex Endl. Gen. 331. 1837.

Nectandra decandra Roxb. Hort. Beng. 90. 1814 (TYPE: *Roxburgh s.n.*!); Fl. Ind. **2**: 425. 1832.
Linostoma decandrum (Roxb.) Wall. Cat. n. 4203. 1831, sine descript.

Subscandent to scandent shrubs or lianas (?) to 15 m. tall; young stems terete, dark reddish brown, glabrous except for a few short trichomes in the leaf axils, the lenticels round, becoming horizontally elongate; axillary branches normal or rarely modified and unciform, the unciform branches usually conspicuously swollen basally. Leaf blade lanceolate or elliptic to oblong-elliptic, 3.5–10 cm. long, 1.5–3.5 cm. broad, acute or acuminate to subcaudate at the apex, cuneate to obtuse at the base, thick-coriaceous, glabrous, darker above than beneath, the costa immersed above, elevated beneath, the primary lateral veins many, inconspicuous, parallel and more or less straight, the submarginal vein well developed, almost coinciding with the margin; petiole canaliculate, rugose, glabrous, 3–5 mm. long. Inflorescences borne terminally on the young shoots, generally involving several nodes, often compound; each inflorescence 3–7(–12)-flowered, subracemiform to rarely umbelliform, glabrous, the primary peduncle 2.7–5.5 cm. long, often with the reduced leaf of the subtending node near the base, the rachis 1–5 mm. long, the secondary peduncles 2–7 mm. long, often distally dilated, the bracts opposite or subopposite, borne at the middle of the primary peduncle or below, ovate, elliptic or oblong-elliptic, 2.5–4.5 cm. long, 1–2 cm. broad, obtuse to acute at the apex, truncate to rounded at the base, almost membranaceous, glabrous, creamy white, venation much more lax than that of the leaves,



MAP I. Distribution of the species of *Linostoma*: dots, *L. decandrum*; triangles, *L. persimile*; squares, *L. pauciflorum*.

subsessile, the bracteole borne at the summit of the primary peduncle, narrowly linear, 0.3–1 cm. long, caducous. Calyx tube fusiform, 5–7(–13) mm. long, 2–2.5 mm. in diameter at the orifice, glabrous and reddish without, villous and white within but often glabrous in the lower half, the trichomes protruding from the orifice; calyx lobes linguiform, 6.5–8.5 mm. long, 2–2.5 mm. broad, as long as or longer than the calyx tube, glabrous, strongly reflexed; petals inserted at the orifice, clavate, erect, fleshy, exserted, 3.5–6 mm. long, apex irregular, their bases connate by means of an obscure annulus; stamens exserted beyond the petals, inserted in a single whorl immediately below the petals, the filaments filiform, glabrous, the antisepalous filaments 6.5–9 mm. long and slightly longer than the alternisepalous ones, the alternisepalous filaments 4–8 mm. long, the anthers oblong, about 1 mm. long, 0.75 mm. broad, the connective basally inflated but not produced beyond the pollen sacs, the pollen sacs appearing confluent and hippocrepiform following anthesis; disc of small, irregularly shaped lobes, more or less adnate to the calyx tube, less than 0.5 mm. tall, each lobe glabrous or more often bearing a number of short trichomes; stipe and ovary ellipsoid, about 3 mm. tall, densely sericeous, the style filiform, 8–11 mm. long, sericeous at the base, otherwise glabrous, the stigma mammiform, exserted beyond the anthers, about 0.75 mm. in diameter; pedicel 3–4.5 mm. long, glabrous. Fruit (immature?) ovoid, 8–12 mm. long, 4–8 mm. in diameter, sericeous, dull red, the longitudinally and unilaterally ruptured calyx tube more or less persistent at the base; pedicel 5–7 mm. long, somewhat swollen.

ILLUSTRATIONS. Denkschr. Bot. Ges. Regensburg 3: *t. 7.* 1841; Baillon, Hist. Pl. 6: 104. *figs. 72, 73.* 1877; Pflanzenfam. III. 6a: *232. fig. 82. A–E.* 1894; Lecomte, Fl. Gen. Indo-Chine 5: 173. *fig. 16.* 1915; Bibl. Bot. 27(111): *t. 2, fig. 11.* 1934.

DISTRIBUTION. Eastern India, East Pakistan, Burma, Thailand, Vietnam, Laos, and Cambodia, the plants associated with evergreen scrub or forests, collected at altitudes up to 200 meters. Flowering specimens collected in January, April, June, November and December, specimens in fruit collected in December and February. Roxburgh (Fl. Ind. 2: 425. 1832) says that the plants flower in October and the seeds ripen in January, February and March.

India. WEST BENGAL: Calcutta, (cultivated?), *Gaudichaud 324* (GH). MANIPUR: Piphima, *Meebold 5164* (G). ASSAM: Sialsuk, Lushai Hills, *Parry 410* (K). **East Pakistan.** EAST BENGAL: Sylhet, *Wallich 4203* (BM, G, L, M), *Roxburgh* "1813" (BM, G), "1830" (K), without collector, (G, L, W); Chittagong Division, *Cowan s.n.* (US); Chittagong Hills, *Dr. King's collector 106* (US), *220* (G, L), *Hooker & Thomson s.n.* (BM, G, GH, K, L, M, P, U, W). **Burma.** KACHIN: Myitkyina District, Tagwin, *Parkinson 316* (K); Myitkyina District, hills W. of Hopin, *Parkinson 347* (K); Bhamo, *Cubitt 1047* (A). **Thailand.** CHONBURI: Chonburi, on trail between Mapkhla and Thapsai, *Smitinand 3637* (L); Khow Diu near Sriracha, *Collins A* (BM), *1797* (BM, US). NAKON RATCHASIMA: Hui Reng, Kerat (Korat), *Kerr 17588* (BM); Kao Lem, Korat, *Put 3573* (BM). RAYONG: Ban Pe, Rayawng (Rayong), *Put 2763* (BM). **Vietnam.**

ANNAM: Nha Trang, *Alleizette s.n.* (L); Tourane, *Clemens & Clemens 3465* (P); Col de Braian, Pnom-sapoum, by Blao, *Poilane 23698* (K). **Laos.** CHAMPASSAK: Bassac, *Thorel 2612* (P). **Cambodia.** Insula Phu Quoc, *Pierre 1470* (P), *19794* (BM). **Without Locality.** *Wallich 2247* (C), *Bruce s.n.* (W).

There has been considerable confusion and error as to the proper citation of authorship of the genus and of this, the type species. The generic name was first used by Wallich in 1831 (Cat. n. 4203); this publication consists of the name *Linostoma decandrum* and the citation "Hort. Beng." From this scrap of information it is evident that Wallich intended a "new combination" based on *Nectandra decandra* Roxburgh (Hort. Beng. 90. 1814). Roxburgh included here, in addition to the epithet, the common name, the place of collection, a two-symbol description and the time of flowering. It was not until Endlicher in 1837 (Gen. 331) published a Latin diagnosis for *Linostoma* that either the genus or Wallich's "combination" became valid. The citation of the type species thus should be *Linostoma decandrum* (Roxburgh) Wallich ex Endlicher.

As a result of Roxburgh's publication (1814) he is given credit or rather discredit for an illegitimate genus (*Nectandra* Roxb. non alior) which is usually cited in the generic synonymy. However, in a subsequent publication (Fl. Ind. 2: 425. 1832) he maintains (despite Wallich's combination of which he probably was not aware) the name *Nectandra decandra*, furnishes generic and specific descriptions and attributes the genus to Jussieu! Indeed, Jussieu, in an earlier work (Gen. Pl. 86. 1791), had published an account of the genus *Nectandra* which was based, in turn, on *Nectandra* Berg. and which included a generic description and a single species based on *Gnidia sericea* L. The illegitimate genus *Nectandra* Berg. (Descript. Pl. Cap. 131. 1767) is composed of three previously described 4-merous species which are not congeneric with our 5-merous *Linostoma decandrum*. Thus Roxburgh did not describe a new genus but merely expanded the concept of a previously existing one. That he was in error is of little consequence. Since the citation in generic synonymy of all genera in which species of a particular genus have been misplaced leads to absurdity, these misplacements are adequately and properly cited within the specific synonymy.

There is additional confusion concerning the type specimen. To the best of my knowledge a type has never been selected, although most authors in discussing this species include the citation of *Wallich 4203*. As a result of examining a number of specimens, all labeled *Wallich 4203*, I have come to the conclusion that these collections are a heterogeneous group. Four I believe to be authentic Wallich collections: Munich with a penciled label "4203," probably written by Wallich; Leiden with a penciled "4203"; British Museum with the penciled label "4203, Wallich Nov. 1829," also probably written by Wallich; and finally a Geneva specimen with a printed label "Wallich 1829." There are a number of other specimens which may also be Wallich collections, for they bear the "Catalogue" number, but I suspect that these specimens were either collected after the publication of the "Catalogue" or that the number was added

to earlier collections as a means of specific identification, regardless of the collector. Some examples are specimens at Leiden and Geneva which bear the "Catalogue" number, but lack collection data, and a specimen from Kew which bears the "Catalogue" number, but the date 1830. There is also a collection at Vienna which bears a printed label upon which in red ink the "Catalogue" number, epithets, place of collection and collector (H. Bruce) have been added. Therefore, it seems that considerable caution must be used in evaluating specimens bearing the "Catalogue" number. However, in spite of past inference, the Wallich collections do not contain the type among them! The type must be selected from the collections of Roxburgh made prior to 1814. I have seen two specimens which probably qualify: one from the Geneva herbarium with a handwritten label, "Nectandra decandra Roxb., Ex Sylhet montibus," and, on the same label and written at a later date in another hand, "Linostoma dicandrum. Wallich"; a second specimen from the British Museum bears a label written in ink, almost certainly by Roxburgh, "Nectandra decandra probably a *Dais*, or in all events a Thymeleae." Added below in pencil is the notation "Roxburgh 1813." Inasmuch as the British Museum specimen appears to be best qualified I select it as the lectotype. It is composed of two flowering branchlets and a packet containing inflorescences, flowers and very immature fruit.

2. **Linostoma persimile** Craib, Kew Bull. 1911: 452. 1911 (TYPE: *Kerr 814*!).

Shrubs to 1.5 m. tall; young stems slender, terete, light brown to reddish brown, glabrous, the lenticels inconspicuous; axillary branches normal or sometimes slightly recurved. Leaf blades rotund, broadly elliptic to obovate, 2–3 cm. long, (0.8–)1–2.5 cm. broad, mucronulate and obtuse, truncate, or retuse at the apex, cuneate at the base, thin-coriaceous, glabrous, darker above than beneath, the costa immersed above, elevated beneath, the primary lateral veins many, parallel and more or less straight, the submarginal vein inconspicuous, almost coinciding with the margin; petiole shallowly canaliculate, slightly rugose, glabrous, 1–2 mm. long. Inflorescence borne terminally on the young shoots, involving a few to several nodes, sometimes compound; each inflorescence 3–6-flowered, umbelliform, glabrous, the primary peduncle 2–4 cm. long, often bearing the reduced leaf of the subtending node near the base, the rachis about 1 mm. long, the secondary peduncles at most 0.5 mm. long, distally dilated, the bracts subopposite, borne at the middle of the primary peduncle or below, ovate to elliptic, 2–3 cm. long, 1–2 cm. broad, acute and mucronulate at the apex, obtuse to subcordate at the base, membranaceous, glabrous, with a venation more lax than that of the foliage leaves, the bracteole borne at the summit of the primary peduncle, linear, about 1 mm. long, caducous. Calyx tube tubular, 8–10 mm. long, 2–3.5 mm. in diameter at the orifice, glabrous without, glabrous within, yellow; calyx lobes linguiform, 4–4.5 mm. long, 1.5–2.5 mm broad, much shorter than the calyx tube, glabrous, erect or slightly spreading; petals inserted

at the orifice, liguliform, erect, exserted beyond the anthers and the stigma, 3–3.5 mm. long, gradually tapering to the acute apex, fleshy; stamens inserted in two distinct whorls, the filaments filiform, glabrous, the antisepalous filaments about 1 mm. long, the alternisepalous filaments to 0.5 mm. long, the anthers oblong, 0.75–1 mm. long, 0.5 mm. broad, the connective obtusely produced beyond the pollen sacs, the upper antisepalous filaments inserted just below the petals, exserted, the lower alternisepalous filaments inserted about an anther's length below the antisepalous ones, included; disc of minute irregular lobes, adnate to the calyx tube, glabrous; stipe and ovary ellipsoid, about 2 mm. long, 0.75 mm. in diameter, densely sericeous, the style filiform, 6–7.5 mm. long, glabrous, the stigma capitate, exserted beyond the stamens; pedicel 1.5–3 mm. long. Fruit accrescent, surrounded by the persistent calyx, the calyx more or less narrowly lageniform, 11–13 mm. long, 5–7 mm. in diameter, the lobes erect, the drupe broadly fusiform, 7–9 mm. long, 6–7 mm. in diameter, sericeous at least towards the apex; pedicel slightly swollen.

DISTRIBUTION. Burma and Thailand. Collected at altitudes of from less than 50 meters to 1650 meters. Found in deciduous forest or open "pine jungle." The collections indicate flowering in September, November, and December, with fruiting known in November and December.

Burma. KARENNI: Karen Country and Hills, *Kurz 990* (M). **Thailand.** CHIENGMAI: Camp Hoi Chan Kiang, Doi Sootep, *Rock 123* (US); summit of Doi Chom Cheng, Doi Sootep, *Rock 1173* (US); Doi Sootep, *Garrett 1397* (A, L, US), *1436* (K, L), *Kerr 814* (K-holotype, BM), *s.n.* (BM). **Without precise locality:** Tung Quang, Petchabuni (?), *Kerr 20584* (BM), *Marian 2759* (K).

The collections *Kerr 20584* and *Marian 2759* have not been mapped for I am not certain of the spelling of the locality on the handwritten labels, which read either "Petchabuni" or "Petchaburi." Since a distance of about 250 miles separates these two cities, it seems best not to make a judgment at this time. If an itinerary of Kerr's travels exists, the location could probably be determined.

The holotype has with it a packet containing a rather unusual flower. This flower, which is nearly mature, has two petals (both lateral with respect to the single calyx lobe which they flank) which have become connate below by their lateral margins. In addition, these fused petals have produced a smaller subsidiary petal between them. The stamen standing in front of this petalaceous anomaly is unusual in that the filament is almost hispid, in striking contrast to the glabrous filaments of the remaining nine stamens. The position of the stamen, i.e., standing within this petalaceous anomaly, provides evidence by its gross morphological position, of the true petalaceous nature of this structure.

A number of flowers in several collections display an included stigma. Close examination indicated that the elongation of the style is delayed until after the pollen is shed. I assumed that this might be some form of mechanism for the prevention of self-pollination, specifically, proterandry. However, Burrows (1960) has described a somewhat comparable

mechanism in the genus *Pimelea* and his observations and conclusions may be applicable to this species. In essence, he found that in bisexual flowers early pollination inhibited elongation of the style, with the result that fertilization may take place and the style remained included, late pollination inhibited elongation to a lesser degree, even though fertilization could no longer occur, and, finally, the lack of pollination allowed the style to elongate greatly and thus the stigma to become well exserted.

3. **Linostoma pauciflorum** Griffith, Calcutta Jour. Nat. Hist. **4**: 234. 1844 (TYPE: *Griffith 4376*!).

Linostoma leucodipterum Hallier f. Med. Rijksherb. **44**: 28. 1922 (TYPE: *Hallier f. B.2261*!).
Linostoma longiflorum Hallier f. *ibid.* 29 (TYPE: *Haviland 1759*!).

Shrubs, trees, or climbers, to 25 m. tall; young stems filiform to slender, terete, light to dark brown, glabrous except for a tuft of short trichomes in the leaf axils, the lenticels inconspicuous; axillary branches normal or gently to strongly uncinate, becoming swollen at the base. Leaf blade ovate, lanceolate, narrowly to broadly elliptic or oblong-elliptic, 1–5 cm. long, 0.5–2.5 cm. broad, mucronate and acute, obtuse, truncate or retuse at the apex, cuneate to obtuse at the base, thin-coriaceous, glabrous, but sometimes appearing farinose beneath, darker above than beneath, the costa plane to immersed above, plane to elevated beneath, the primary lateral veins numerous, more or less straight and parallel, inconspicuous, the submarginal vein well developed, coinciding with the margin; petiole canaliculate (although sometimes scarcely so), 1–3 mm. long, rugose, glabrous. Inflorescences borne from the axils of the terminal portions of the young stems, simple or compound, glabrous except for occasional trichomes near the summit of the primary peduncle; each inflorescence 1–5-flowered, umbelliform, the primary peduncle 2–18(–30) mm. long, often with the reduced leaf of the subtending node near the base, the rachis to 0.5 mm. long, the secondary peduncles obsolete, to 0.5 mm. long, somewhat dilated distally, the bracts borne from the middle to the summit of the primary peduncle, opposite, subopposite, or alternate, foliaceous or reduced and bracteolate, linear, lanceolate, ovate, elliptic or oblanceolate, 2–35 mm. long, 2–18 mm. broad, mucronulate and acute, obtuse, or truncate at the apex, acute, obtuse, or subcordate at the base, membranaceous, glabrous, white, the venation more lax than that of the foliage leaves, the bracteole borne at the summit of the primary peduncle, linear, to 10 mm. long, sometimes caducous, or extremely reduced and represented by a small lump of tissue in the axil of which stand a few trichomes. Calyx tube tubular to ellipsoid, 7–25 mm. long, about 0.5 mm. in diameter at the orifice, glabrous and green to white without, glabrous or partially to completely villous within, a few trichomes exserted beyond the orifice; calyx lobes lanceolate or elliptic to oblanceolate, 3–12 mm. long, 1.5–3 mm. broad, usually glabrous, spreading; petals inserted at the orifice, narrowly clavate,

fleshy, exserted, erect, 5.5–7.5 mm. long, obtuse to irregular at the apex, glabrous; stamens inserted in two close whorls just below the petals, exserted beyond the petals, the filaments filiform but enlarging distally, 4.5–10 mm. long, glabrous, the antisepalous filaments somewhat longer than the alternisepalous ones, the anthers more or less oblong, 0.5–1 mm. long, 0.5–0.75 mm. broad, the connective enlarged so as to displace the pollen sacs to its lateral margins but not produced beyond the pollen sacs; disc annular, with irregular lobes, 0.25–0.5 mm. high, glabrous; ovary and stipe oblong-obovoid or obovoid, 3–7.5 mm. long, sparsely to densely sericeous, the style filiform, 6–20 mm. long, glabrous or with occasional trichomes, the stigma capitate, exserted beyond the stamens; pedicel 5–8 mm. long. Calyx tube accrescent in fruit, ellipsoid but tapered more sharply above than below, 12–15 mm. long, 6–7 mm. in diameter, the drupe ovoid.

ILLUSTRATION. Flora Malesiana I. 6: *26. fig. 11.* 1960 (as *L. longiflorum* and *L. pauciflorum*).

DISTRIBUTION. Thailand, south to Singapore and east to Borneo; collected from sea level to 200 meters. Flowering in March, April, June, August, September, and October; collected in fruit in December. Found in evergreen scrub, wastelands, and primary peat forests; the Hillard collection is from "undergrowth on rubber estate."

According to Kerr the root is sometimes used for poisoning fish.

Thailand. PATTANI: Yala, *Kerr 7258* (BM); Kok Po, *Kerr 15073* (BM). SONGKHLA: Hạt Zai, *Kerr 13667* (BM). SURATTHANI: Surat, *Kerr 11302* (BM), *Kerr 11820A* (BM). LOCALITY UNCERTAIN: Tako, Qungsuam (?), *Kerr 11870* (BM). **Malaya.** KEDAH: Langkawi Islands, *Curtis s.n.* (P), *Hillard KL1411* (A); Langkawi, Palo Lingsong (?), *Curtis*, 1890 (BM). PERAK: Pangkore Island, *Scortechini 983* (K), *Burkill & Shah HMB 240* (K, L). PERLIS: Chapnema (?), *Ridley 14916* (BM). YALA: Pulau Penang, Telok Bahang, Toi, 1905 (BM), *Sinclair SFN 39304* (L). WITHOUT LOCALITY: *Maingay 1308/3* (L). **Singapore.** *Griffith 4376* (K-holotype of *L. pauciflorum*); Changi, *Ridley 1858* (BM); Botanic Gardens, *Kiah SFN 37931* (BM, L). **Sarawak.** Kuching, *Haviland 1759*, Oct. 1892 (L-holotype of *L. longiflorum*; BM, GH, K), *Brooke 9696* (G, L); Binatang, *J.A.R. Anderson 9047* (L); Tanjong Po, *Brooke 10603* (G); near Long Kapa, Mount Dulit (Ulu Tinjar), *Richards 1312* (A, K). **British North Borneo.** Sandakan and vicinity, *Ramos 1799* (A, US); Gaya Island, *Haviland 1440* (K). **Borneo.** W. BORNEO: zwischen Súngai Dějmělá und Gûnûng K(e)lamm, *Hallier B.2261* (isotypes of *L. leucodipterum*, L, P).

My treatment of this group of specimens as a single species requires more than a perfunctory explanation because of the recent work of Hou (1960) for the *Flora Malesiana* in which the treatment differs. Geographically, the specimens can be divided into two groups, one restricted to the island of Borneo and the other to peninsular Malaya. I shall discuss the relationship of the Bornean specimens to each other and to peninsular specimens (when of some significance).

Hou (1960) has recognized two species from Borneo, *Linostoma pauciflorum* and *L. longiflorum*. His key to these species is based upon differ-

ences in the bracts, particularly the size and the degree to which they cover the lower half of the calyx tube, as well as the length of the calyx tube. On the basis of his key I have seen two collections which clearly can be placed with *L. longiflorum*; they are *Haviland 1759* (type of *L. longiflorum*) and *Anderson 9047*. In addition, *Jahri 166* may belong with this unit, but the Leiden specimen examined lacks inflorescences. It has been annotated by Hou as *L. longiflorum*, and he may have seen a more complete specimen from the Bogor herbarium.

The leaves of the two "species" are extremely variable in shape and size, although the leaves of *Haviland 1759* tend to be the broadest of all Bornean collections (but no broader than those found on some of the peninsular specimens). There appears to be no certain way to separate two species on the basis of either leaf shape or size.

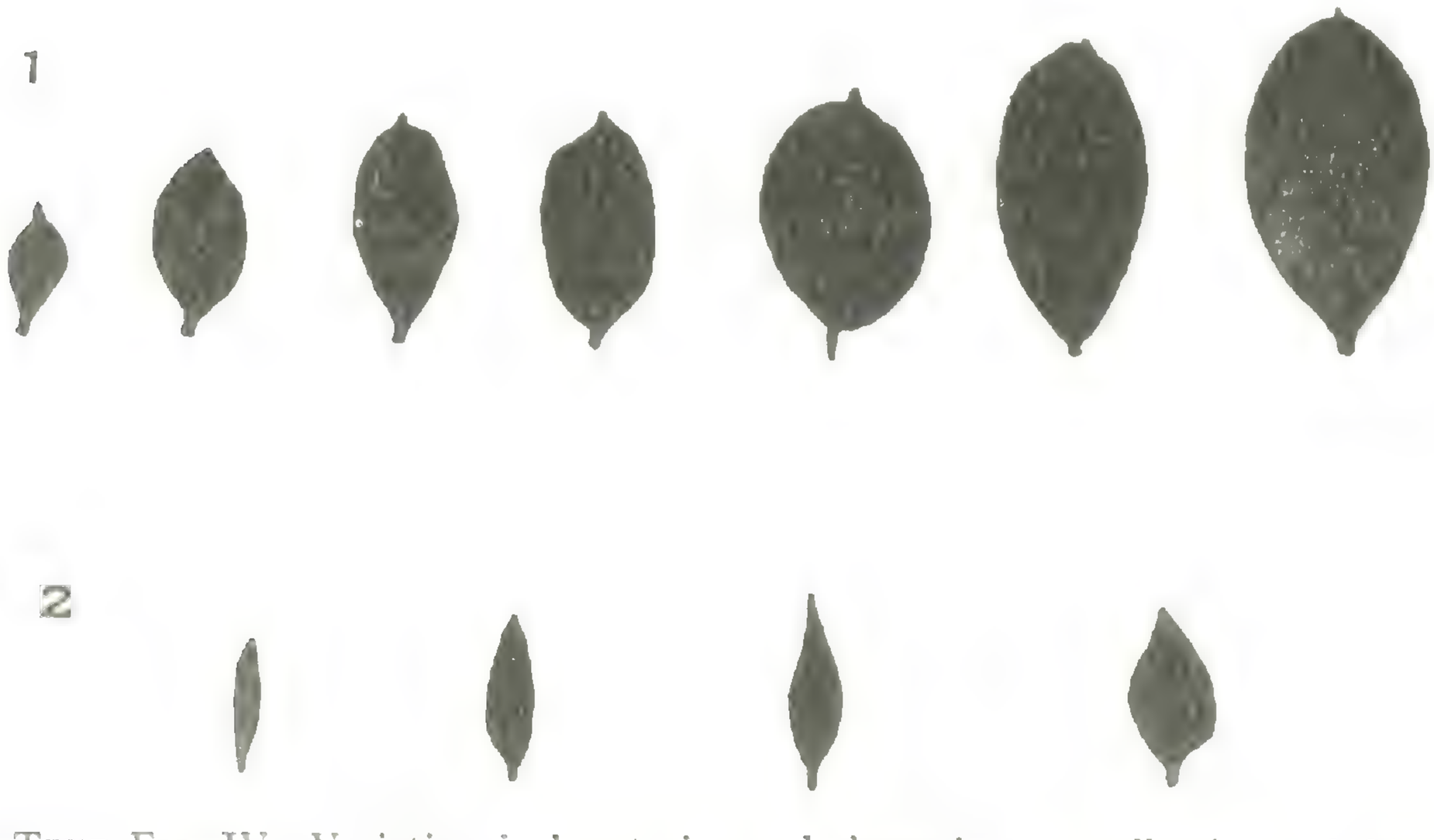
As already indicated in the introductory comments, the structure of the leaf is rather constant throughout the genus, but several characteristics in this connection are of interest. The stomata of this species are similar to those of *Linostoma persimile* but quite different from those of *L. decandrum*. The lower leaf surface often appears farinose under magnification. This phenomenon is due to the papillate shape of the outer periclinal wall of individual cells of the lower epidermis. This condition can be demonstrated to a greater or lesser degree in most of the collections, either peninsular or insular and including the type of *L. longiflorum*, but is not found elsewhere in the genus. Finally, it must be mentioned that Hallier in the original description of *L. longiflorum* made reference to a fungal infection in the type. It was thus a surprise to find the leaves of *Anderson 9047* similarly affected. None of the Bornean collections referable to *L. pauciflorum* (by Hou's system) appears, on the basis of cleared leaves, to be infected, and to draw a conclusion is almost irresistible.

The basic structure and size of the inflorescence is essentially the same in both "species," although there are certain differences which require discussion. In *Linostoma longiflorum* the number of flowers per inflorescence is one, whereas in *L. pauciflorum* it is rarely one, generally two (Borneo), and sometimes as many as five (peninsular). There does not seem to be any real correlation between the number of flowers per inflorescence and their size as one might expect to find.

The position of the bracts near the summit of the primary peduncle is the same in all Bornean specimens. In the peninsular specimens, in which the bracts are alternate, one of the pair is borne at the summit of the primary peduncle. This distal position of the bracts gains importance because it is unique within the genus (other species having the bracts borne at the middle of the primary peduncle or below).

The importance of the bracts themselves is magnified by their use as a "key" character. In *Linostoma longiflorum* the bracts vary in length from 2–12 mm. and their shape is usually linear or linear-lanceolate. The bracts of specimens referable to this species which I have cleared seem to have a poorly differentiated vascular system, perhaps an indication that growth of the bract had ceased before attainment of "mature" form. The

bracteole, in contrast, is well developed. In *L. pauciflorum* the bracts vary from 8–35 mm. in length, and the shape, although variable, is considerably broader than that found in *L. longiflorum*. The bracteole, in contrast, is poorly developed and is sometimes reduced to only a small lump of tissue in the axil of which stands a tuft of trichomes. It is tempting to consider a type of developmental anomaly which indiscriminately "stunts" the growth of the bracts (*L. longiflorum*) on the one hand and growth of the bracteole (*L. pauciflorum*) on the other.



TEXT FIG. IV. Variation in bract size and shape in two collections of *Linostoma pauciflorum*: 1. *Hallier B.2261*, from Borneo; 2. *Haviland 1759*, from Sarawak (Natural size).

Outlines of a series of bracts showing extremes in variation from two collections representing *Linostoma longiflorum* (*Haviland 1759*) and *L. pauciflorum* (*Hallier B.2261*) are presented in TEXT FIG. IV. It is of more than casual interest that a size overlap occurs and that the largest bract in the Haviland collection is quite similar in shape to the smallest bract found in the Hallier collection. Additional collections from Borneo will be necessary before this problem of size variation and overlap can be evaluated. It should be obvious at this point that the degree to which the bracts cover the base of the calyx tube is determined by the length of the bracts. This does not mean that the key does not work in the area of overlap. There are generally enough bracts on the available specimens to indicate strikingly to which "species" the specimen belongs, but I think that it does detract from the validity of this key character.

Generally speaking, the vegetative portions of a plant may be expected to be more variable than reproductive structures. To check this generality a study of morphological and, to a lesser degree, anatomical characteristics of the flower was made. As in the case of the leaves, the sample is extremely small, but the floral characteristics showed a striking homo-

geneity which cannot be easily dismissed. The calyx tube is the same shape and has the same type of pubescence in all Bornean collections. In flowers of insular specimens the calyx tube is variously villous within and is in sharp contrast to those of the peninsula in which the calyx tube is glabrous within. This difference is not considered taxonomically significant. The length of the calyx tube (a key character) is variable but it does not have a comparable overlap as found in bract size. In *Linostoma pauciflorum* it varies from 13–15 mm. in length (insular) and from 7–15 mm. in length (peninsular), whereas in *L. longiflorum* it varies from 17–25 mm. in length. Tube measurements must be taken from flowers at anthesis as there is considerable elongation of the tube immediately prior to anthesis. The occasional oblanceolate shape of the calyx lobes is a character shared by both "species" and is unique within the genus. The margin of the calyx lobe is sometimes furnished with a few very small trichomes in *L. pauciflorum* (both insular and peninsular) but I have not seen them in the two collections referable to *L. longiflorum*.

The petals of the two are alike in shape, size, insertion, and degree of exsertion. Indeed, in the original description of *Linostoma longiflorum* Hallier says of petals and stamens, "fere ut in sp. praecedente" (*L. leucodipterum*,* synonymous with *L. pauciflorum*). The most striking point is that the petals are vascularized by a single vascular strand, a condition that is once again unique within the genus (the other species lacking vascularization of the petals altogether).

Similarities within the androecium are also to be found as indicated by Hallier's original description of *Linostoma longiflorum*. The insertion of the stamens and their relative exsertion is the same in all specimens. The peculiar swelling of the filament towards its summit is common, as is the very expanded connective. (The connective is enlarged to the extent that the pollen sacs are displaced to its lateral margins and one wonders whether or not the dehiscence can be spoken of any longer as introrse.) Examination of the pollen shows similar size and sculpturing of the exine (which is, however, rather constant throughout the genus). The disc is the same type in all specimens.

The gynoecium is notable for the very long stipe (longest in the genus) which gradually tapers into the ovary. The pubescence of the stipe and ovary is similar and differs from other species in that the trichomes tend to be shorter and blunter. However, it is in the vascularization of the ovary that the soundest factual homogeneity is found. That is not to say there is no variation in the specimens of this species, for there certainly is, but it is the kind of variation that is indicative of a basic relationship. A series of camera lucida drawings made from cleared and stained ovaries from *Ridley 1858* (representative of peninsular *L. pauciflorum*), *Hallier B.2261* (isotype of *L. leucodipterum*) and *Haviland 1759* (isotype of *L. longiflorum*) is presented in TEXT FIG. III, *3–5*. In all three examples a well-developed ovular trace is present, in contrast to the very poorly developed or obsolete (?) ovular trace of other species

* Holotype deposited at Bogor and not seen by me, isotypes at Leiden and Paris.

(see TEXT FIG. III, *1*, *2*). In addition, the number of accessory traces is notably decreased and a trend of reduction within the series itself seems a remote possibility.

In summation, the combination of shared morphological and anatomical characteristics which are often unique within the genus is overwhelming evidence of the conspecific nature of this group. In addition, I think that the dissimilarities noted, which are of a quantitative and not a qualitative type, fall within the range of variation that could be expected within a single species of this family.

STATUS UNDETERMINED

Psilaea Miquel, Fl. Ind. Bat. Suppl. 355. 1860 (TYPE: *P. dalbergioides*).

Psilaea dalbergioides Miquel, *ibid.* (TYPE: *Teysmann* ?).

This genus and species were based by Miquel on a Teysmann collection from Siboga [sic, Sibolga], Sumatra. Presumably the specimen would be deposited in the herbarium at Utrecht but no record can be found of it there at present.

Kurz (1870, p. 82, 83) in a discussion following the description of *Linostoma siamense* says that he has authentic specimens of the type species (*Psilaea dalbergioides*) and "cannot see how the species should differ from Linostoma pauciflorum, Griff." From his short discussion two important conclusions can be drawn: (1) that Kurz did not distinguish between *Linostoma* and *Enkleia*; (2) that he had an authentic specimen during his curatorship at the Royal Botanic Gardens, Calcutta. I have not yet determined whether this specimen is extant at Calcutta.

This species has been referred repeatedly to the synonymy of *Linostoma pauciflorum*. I feel that this action is the result of Kurz's comments, and that it involved no subsequent investigation. Inasmuch as Kurz did not distinguish between *Linostoma* and *Enkleia* I prefer to defer a decision regarding this name until the type is located or authentic specimens from Sumatra may be examined. I have not seen any specimens from Sumatra referable to the genus *Linostoma* to date, although Hou (1960) gives Simalur as a locality for *L. pauciflorum*.

Linostoma sect. **Psilaea** (Miq.) Hallier f. Med. Rijksherb. no. 44, 28. 1922.

Hans Hallier (1922) when treating the genus *Linostoma* split it into two sections: *Eulinostoma* Meissner, including only *L. decandrum*, and *Psilaea*, presumably based on Miquel's *Psilaea dalbergioides* as indicated by parenthetical credit, including Hallier's two new species *L. leucodipterum* and *L. longiflorum*. Although his brief descriptions would fail to hold today and infrageneric categories, with the exception of species, are considered unnecessary in view of the small number of species, his concept was in essence correct. *Linostoma decandrum*, on the basis of several

morphological characteristics, stands isolated from *L. persimile* and *L. pauciflorum*.

Linostoma incertae sedis

A collection from Brunei, *Ashton BRUN 573*, has caused me considerable concern. It is an immature flowering specimen which is somewhat abnormal due to a fungal infection. The original identification was "Linostoma leucodipterum Hall. f.," subsequently modified to "Linostoma pauciflorum Griff." by Hou (annotation, 1958, and Identification Lists of Malaysian Specimens, July, 1960). Superficially it does resemble this species, but closer examination shows some differences, such as general pubescence, position of the inflorescence, number of flowers per inflorescence, lack of a disc, and pubescence and shape of the ovary. I should not be surprised to find that it represents an undescribed species but believe that any taxonomic designation at this time would be premature. I have, however, taken the liberty of including here a description which the reader will appreciate as being lacking in many respects.

Climber to 25 m. tall; young stems generally slender, terete, ferrugineously tomentulose and glabrescent, the lenticels inconspicuous; axillary branches normal. Leaf blades ovate to lanceolate, 2–4.5 cm. long, 1–2 cm. broad, acute to obtuse at the apex, cuneate to obtuse at the base, chartaceous, glabrous, except for occasional trichomes beneath, darker above than below, the costa immersed above, elevated beneath, the primary lateral veins many, parallel and more or less straight, the submarginal vein well developed, coinciding with the margin; petiole canaliculate, sparsely tomentose, 1–3 mm. long. Inflorescences simple, borne terminally on the young stems or axillary branches, (5–)10–16-flowered, sparsely tomentose, the primary peduncle 2–3 cm. long, the rachis 1–2 mm. long, the secondary peduncles about 0.5 mm. long, the bracts (with fungal infection) borne below the middle of the primary peduncle, opposite or subopposite, narrowly elliptic, 2–3 cm. long, 0.5–1 cm. broad, obtuse at the apex, cuneate at the base, membranaceous, sparsely puberulent both surfaces, the bracteole borne at the summit of the primary peduncle, linear, 0.5–2 mm. long. Immature flowers: calyx tube short-tubular, 1–3.5 mm. long, 0.5–1.5 mm. in diameter at the orifice, sparsely strigose without, glabrous within, cream-colored; calyx lobes ovate, 1 mm. long and broad, erect, glabrous within; petals inserted at the orifice, linguiform, 1–2 mm. long, ca. 0.75 mm. broad, acute at the apex, glabrous, exserted beyond the stamens; stamens borne in 2 whorls, the antisepalous whorl inserted just below the petals, exserted, the alternisepalous whorl about an anther's length below the antisepalous whorl, included, the filaments 0.5–0.75 mm. long, glabrous, the anthers oblong, to 0.5 mm. long and broad; disc absent; ovary ovoid, ca. 1 mm. tall, densely hirsute, style and stigma poorly differentiated; pedicel to 4 mm. long.

Brunei. Collected in September in primary forest, altitude 50 meters, Andulau F. R., *Ashton BRUN 573* (L).

EXCLUDED TAXA

LINOSTOMA subg. LINOSTOMA Kurz, Jour. As. Soc. Bengal 39(2): 83. 1870, as to species cited. = **Enkleia** Griff.

LINOSTOMA sect. LOPHOSTOMA Meissn. in Mart. Fl. Bras. **5**(1): 72. 1855 (Type: *L. calophylloides* Meissn.) = **Lophostoma** Meissn.

LINOSTOMA ALBIFOLIUM Rodr. Vellosia 1885–88. ed. 2. 67. *t. 20.* 1891 = **Lophostoma albifolium** (Rodr.) Gilg in Engl. & Prantl Nat. Pflanzenfam. III. **6a:** 232. 1894.

LINOSTOMA ANDAMANICA Hutchinson ex C. E. Parkinson, Forest Flora Andaman Isl. 2291. 1923 = **Enkleia** sp.

LINOSTOMA CALOPHYLLOIDES Meissn. in Mart. Fl. Bras. **5**(1): 72. 1855 = **Lophostoma calophylloides** (Meissn.) Meissn. in DC. Prodr. **14:** 600. 1857.

LINOSTOMA DINIZII (Huber ex Ducke) Lemee, Fl. Guyan. Fr. **3:** 108. 1953 = **Lophostoma dinizii** Huber ex Ducke, Arch. Jard. Bot. Rio de Janeiro **1:** 51. 1915.

LINOSTOMA SCANDENS (Endl.) Kurz, Jour. As. Soc. Beng. **39**(2): 83. 1870 = **Enkleia** sp.

LINOSTOMA SCANDENS var. CAMBODIANA Lecomte, Nat. Syst. **3:** 127. 1915. (Type: *Pierre 511*!) = **Enkleia** sp.

LINOSTOMA SIAMENSE Kurz, Jour. As. Soc. Beng. **39**(2): 82. 1870 (Type: *Teysmann 5986*!) = **Enkleia** sp.

LINOSTOMA THORELII Lecomte, Not. Syst. Paris **3:** 127. 1915 (Type: *Thorel 2823*!) = **Enkleia** sp.

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THE GENERA OF VIOLACEAE IN THE SOUTHEASTERN UNITED STATES [1]

GEORGE K. BRIZICKY

VIOLACEAE Batsch, Tab. Affin. Reg. Veg. 57. 1802, 'Violariae.'

(VIOLET FAMILY)

Herbs [to shrubs (sometimes scandent) or trees] with alternate [rarely opposite], simple, usually stipulate leaves. Flowers [regular or] irregular, bisexual [rarely unisexual or polygamous], 5-merous (except gynoecium), solitary to few in the leaf axils [or in racemose or cymose inflorescences]. Sepals distinct [rarely connate at base], imbricate [or open] in bud, usually persistent. Petals distinct, hypogynous, usually imbricated, unequal [or equal], the lowermost larger than the others and often spurred, saccate, or gibbous at base. Stamens 5, alternipetalous, hypogynous, the lowermost two [or all the stamens] often with a gland-, [scale-], or spur-like nectary on the back (abaxial side) [the glands sometimes connate into a "staminal sheath"]; filaments distinct [or connate]; anthers 2-locular at anthesis, introrse, longitudinally [very rarely transversely] dehiscent, connivent or connate into a sheath around the ovary, the broad connective usually produced beyond the anthers into a membranaceous appendage. Gynoecium 3[rarely 2, 4, or 5]-carpellate, syncarpous; stigma simple [rarely 3–5-lobed]; style simple, terminal, sometimes flexuous in the lower part, [filiform to] columnar or clavate, with variously shaped apex ("stylar head"); ovary superior, 1-locular, with 1–many anatropous ovules on each of 3 parietal placentae. Fruit a loculicidal, 3-valved cap-

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University which has been made possible through the support of George R. Cooley and the National Science Foundation. This treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958) and continued through those in volumes **40–42** (1959–1961). It should be repeated that the area covered by this work is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with any supplementary material in brackets. References which the author has not seen are marked by an asterisk.

The results of the study of Violaceae are somewhat more voluminous than had been anticipated. In order to provide a better understanding of the taxonomic-biological complexes of *Viola* an outline of the subsections has been considered an exceptional necessity. The key for the sections is based chiefly on the shape of the stylar head, a character which at least in some cases is liable to subjective perception and evaluation. The literature on *Viola* is very extensive and the references included are more numerous than usual.

The author is indebted to Dr. Carroll E. Wood, Jr., for his criticism and valuable suggestions, and to Mrs. Gordon W. Dillon, for her careful help in the preparation of the manuscript.

sule [or a berry, very rarely nutlike]. Seeds with endosperm, often carunculate. TYPE GENUS: *Viola* L.

A family of 18 [primarily tropical] genera with about 800 species distributed all over the world. Only *Viola*, *Melicytus*, and *Hymenanthera* occur chiefly or exclusively in the temperate zone, the first being of wide distribution, the two latter centered in New Zealand. Of the remaining genera nine are tropical American, two tropical African, one South Pacific (New Caledonia, Fiji, New Guinea), one Hawaiian, and two exclusively (*Rinorea*, with ca. 260 species) or primarily (*Hybanthus*, with ca. 80 species) pantropical. The family appears to be a very natural one, especially the subfamily Violoideae Melch. (including 17 genera), which is subdivided into the tribes Rinoreae, with regular or slightly irregular flowers (e.g., *Rinorea*, *Gleospermum*, *Rinoreocarpus*), and Violeae, with markedly irregular flowers (e.g., *Hybanthus* and *Viola*).

All the genera appear to be entomogamous, but pollination data have been reported only for *Viola*. Cleistogamy is known only in *Viola* and *Hybanthus*, which have also been investigated in regard to embryology. The cytogenetics of *Viola* have been studied extensively; however, there are available only a few chromosome counts for five additional genera, i.e., *Rinorea*, $2n = 24$ (1 sp.), *Decorsella*, $2n = 20$ (monotypic), *Hybanthus* $2n = 24$ (1 sp.), *Melicytus*, $2n = 32, 64, 96$ (4 spp., 3 vars.), and *Hymenanthera*, $2n = 32, 64$ (6 spp.). Taking into consideration these and the chromosome numbers in *Viola* (*q.v.*) one may assume that the polyploidy may be of wide distribution in the family and probably played an important role in the origin of species. *Anchietea* (South America) and *Decorsella* (Africa) are notable for capsules dehiscing when very young (almost immediately after the pollination of the ovary) so that the seeds mature uncovered.

The family is closely related to Flacourtiaceae and through the latter with Turneraceae, Malesherbiaceae, and Passifloraceae. A relationship with Cistaceae seems probable.

The economic significance of the family is mainly based on the ornamental value of numerous species of *Viola*.

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KEY TO THE GENERA OF VIOLACEAE

Sepals not auricled at base; lowermost petal gibbous at base; anthers connate, the abaxial glands of the two lowermost stamens connate. . . 1. *Hybanthus*.

Sepals auricled at base; lowermost petal spurred at base; anthers connivent, the abaxial spurs of the two lowermost stamens distinct. . . . . 2. *Viola*.

1. **Hybanthus** Jacquin, Enum. Pl. Carib. 2. 1760, nom. cons.[2]

Herbs [to shrubs] with alternate [opposite] leaves. Flowers small [or medium-sized], greenish white [white or blue to violet], pediceled, solitary to few in leaf axils [or in racemose, rarely cymose, inflorescences]. Sepals distinct, imbricate in bud, nearly equal. Petals distinct, imbricate, slightly [or considerably] unequal, the lowermost always largest and gibbous or saccate at base. Stamens with filaments distinct [or connate], each of the 2 [rarely 4] lowermost bearing a nectar gland [or spur] on back (abaxial side), the glands connate into one 2-lobed [or entire] nectary [or distinct]; anthers connate [or connivent] into a sheath inclosing the ovary, each connective prolonged beyond the anther into a membranaceous appendage. Gynoecium 3-carpellate; stigma small, simple; style usually club-shaped, the apex hooked [or slightly curved], with stigmatic opening directed forward [abaxially]; ovary 1-locular; ovules 2-integumented with a thick nucellus, 3 [to numerous] on each placenta. Capsule 9[–many]-seeded; seeds relatively large, globose [or ovoid], carunculate, with copious endosperm and large, straight, axile embryo with flat cotyledons. (Including *Cubelium* Raf., *Ionidium* Vent., *Solea* Spreng.) TYPE SPECIES: *H. havanensis* Jacq. (Name from Greek, *hybos*, hump-backed, and *anthos*, flower, referring to the gibbous flowers.)

A largely pantropical genus of about 80 species centered in tropical South America but extending into the Temperate Zones in Uruguay, Argentina, and Chile, in southern Australia, and in North America. The northernmost species is *Hybanthus concolor* (T. F. Forst.) Spreng. (*Cubelium* Raf., *Ionidium* Benth. & Hook. f. ex S. Wats., *Solea* Ging. ex DC.), green violet, a perennial herb with alternate leaves and small greenish-white flowers solitary in two's or three's in the leaf axils, which ranges from Georgia to Mississippi, Arkansas, and Kansas, northward to Wisconsin (?), Michigan, southern Ontario, New York, and Connecticut. Two other species, *H. verticillatus* (Ort.) Baill. (*H. linearis* (Torrey) Shinners) and *H. attenuatus* (Humb. & Bonpl.) G. K. Schulze reach their

[2] Conservation unnecessary; see Rickett & Stafleu, Taxon **8**: 314. 1959.

northern limits westward beyond our range in Kansas and Colorado and in southern Arizona, respectively.

The occurrence of small, cleistogamous flowers with petals reduced or wanting and with two or five glandless stamens has been recorded in *H. concolor* and in the South American *H. communis* (St. Hil.) Taub. and *H. Ipecacuanha* (L.) Baill. Only *H. parviflorus* (L. f.) Baill., $2n = 24$, has been investigated cytologically. The rhizome and roots of *H. Ipecacuanha* have sometimes been used as a substitute for true ipecac (*Cephaëlis Ipecacuanha* (Brot.) A. Rich., and *C. acuminata* Karst., Rubiaceae), an emetic. Roots of several other species are used locally in South America and Asia as emetics and against diarrhea. Although the genus includes spiny shrubs to rosette plants, the delimitation of subgeneric categories awaits a much-needed taxonomic revision. *Hybanthus* is presumably most closely related to *Viola* (Melchior).

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2. **Viola** Linnaeus, Sp. Pl. **2**: 933. 1753; Gen. Pl. ed. 5. 402. 1754.

Herbs [rarely shrubs or subshrubs], often acaulescent, with alternate, petioled [or sessile] leaves. Flowers usually on 1-flowered, solitary peduncles borne in the axils of cauline leaves or (in acaulescent species) directly from the rhizome and stolons; cleistogenes often following the normal, chasmogamous flowers. Sepals subequal, auricled at base. Petals unequal, the lowermost the largest and spurred at base. Stamens with short, distinct filaments, the 2 lowermost bearing spurlike [or wartlike] nectaries projected into the spur of the lowest petal; anthers usually connivent into a sheath inclosing the ovary, each connective produced at apex into a conspicuous, membranaceous appendage; pollen 3(4–6)-colpate, spheroidal to ellipsoidal, smooth, medium-sized to large. Stigma

simple, terminating a stylar beak or situated on the abaxial side, rarely on the summit, of the beakless stylar head; style ± columnar, curved ± forward (rarely upward) at apex, terminating in a beak (rostrum), or enlarged upward into a ± capitate, sometimes margined and helmet-like [or variously appendaged], abaxially beaked or beakless stylar head; ovules 3–many on each placenta, 2-integumented, with a thick nucellus. Seeds globular to obovoid, usually smooth, often carunculate; endosperm copious; embryo straight, axile, with rather thick, plano-convex cotyledons. LECTOTYPE SPECIES: *V. odorata* L.; see Britton & Brown, Illus. Fl. North. U. S. ed. 2. 2: 546. 1913. (Name classical Latin, *Viola*, the digammated form of Greek, *iolon*, a diminutive of *ion*, a violet, or some other flower.)

A genus of about 400 species, of world-wide distribution, centered in the North Temperate Zone, restricted to mountains in the tropics. A few species occur in the Arctic Zone in the Old World and in the Subarctic Zone of North America; the southernmost limits are South Africa, New Zealand (3 spp., 2 endemic), and Tierra del Fuego. Although the Andes of South America abound with endemic species exhibiting a great diversity of floral patterns, only a small number are known from the tropical mountains of the Eastern Hemisphere. The Hawaiian Islands are notable for eight endemic, mostly frutescent (single-stemmed) species (often with racemose inflorescences) which represent a special section, NOSPHINIUM W. Becker (e.g., *V. tracheliifolia* Ging., *V. robusta* Hilleb., $2n$ = ca. 76, *V. mauiensis* Mann, $2n$ = 82, ca. 85, ca. 86). Nearly 80 species in four of fourteen sections recognized by Becker (1925) are represented in North America.

The tentative classification followed below is essentially that of Clausen (1929 and especially 1951) and is based mainly on floral characters (especially the type of stylar head), chromosome numbers, and, to a lesser degree, crossing relationships. The sections given in the key are divided into subsections within which the species are connected by fertile to partially sterile hybrids and between which connections are usually through sterile hybrids. Intersectional hybrids are difficult to produce, and only two instances of vigorous but completely sterile intersectional hybrids are known. No intersectional hybrids involving sect. MELANIUM have been produced. Chromosome numbers have been reported for about 160 species.

KEY TO THE SECTIONS OF VIOLA IN THE SOUTHEASTERN UNITED STATES

A. Upper portion of style variously shaped, beaked or beakless, without a lip-like appendage ("lip") at base of the stigmatic opening; rhizomatous perennials, usually with bractlike stipules.
  B. Style enlarged upward, capitate, beakless, the stigma within a minute opening on the lower (abaxial) side of the stylar head; flowers usually yellow, or white with bases of petals and or spur yellow; usually caulescent. ..... Sect. CHAMAEMELANIUM.

B. Style various, beaked at apex, very rarely beakless; flowers blue to violet, creamy, or white (without any yellow).
C. Style clavate, depressed-capitate and often margined, beaked on the lower side of the stylar head (or in *V. pedata* obliquely concave at summit, beakless); acaulescent. ..... Sect. PLAGIOSTIGMA.
C. Style ± columnar, apex beaked and ± bent or curved forward, rarely almost straight pointing forward and upward; acaulescent or caulescent. ..... Sect. VIOLA.

A. Upper portion of style capitate-globular, beakless, bearing on the lower side a wide stigmatic opening with a "lip" at its base; flowers bluish white, creamy, or lavender (or yellow and/or blue to dark violet); usually caulescent annuals or biennials with large, leaflike, pinnately dissected, ± lyrate, stipules. ..... Sect. MELANIUM.

Section CHAMAEMELANIUM Ging. (sensu Clausen), including North American and Eurasian species forming a polyploid series on a base of six ($2n = 12, 24, 36, 48$ (60), 72), is considered to be the most primitive of the genus (Clausen, 1929). Six subsections occur in North America, three in our area. Subsection *Nudicaules* W. Becker comprises yellow-flowered caulescent violets with one to few basal leaves and stems leafy only toward the summit. The four eastern North American species, *V. pubescens* Ait. ($2n = 12$), *V. eriocarpa* Schwein. (*V. pensylvanica* Michx., fide Fernald) ($2n = 12$), *V. hastata* Michx., and *V. tripartita* Ell., occur in our area. Putative natural hybrids intermediate in morphology and ecology between the first two species have been recorded (Russell, 1960), and the lines between the two are often blurred. Subsection *Canadenses* W. Becker (*Erectae*, *Canadenses* W. Becker) includes North American white-flowered caulescent violets ("Canada violets") represented in our area by *V. canadensis* L. ($2n = 24$), lacking stolons and ranging from Alabama to Tennessee and North Carolina and west- and northward far beyond our area, and the stoloniferous *V. rugulosa* Greene, which reaches its southern limit in northwestern North Carolina and eastern Tennessee. Experimental hybrids between the two are vigorous and fertile, and both intergrade in areas of overlap, suggesting their treatment as parts of a single species (Russell, 1960). Cleistogamous flowers are not produced in this subsection. Subsection *Orbiculares* Pollard sensu stricto (subsect. *Rotundifoliae* Clausen, ined. 1929, not Borbas, 1892) includes only *V. rotundifolia* Michx., $2n = 12$, a yellow-flowered stemless violet, which extends southward along the Appalachians to Georgia and Tennessee. The species is relatively invariable, and there are no indications of hybridization or introgression with other species. This subsection seems to form a transition to sect. PLAGIOSTIGMA (Clausen, 1929). No natural hybrids between subsections have been found, and experimental crosses have either failed or produced dormant seeds or weak seedlings.

Section PLAGIOSTIGMA Godr. (sensu Clausen, 1951) (§ *Nomimium* Ging., in part; § *Nomimium* subsect. *Plagiostigma* auct.) comprises Eurasian and North American white- to violet-flowered acaulescent species forming a polyploid series based on twelve ($2n = 24, 48, 72, 96$), with

some exceptions ($2n$ = 44, 54, 56). Subsection *Primulifoliae* Gershoy (§ *Nomimium*, *Stolonosae* Kupff. sensu W. Becker, in part; § *Plagiostigma* subsect. *Stolonosae* Clausen, 1951; *Stolonosae*, *Primulifoliae* Gershoy) includes usually stoloniferous white violets with slender, cordlike rhizomes, cleistogamous flowers with erect peduncles, and ellipsoid green capsules. *Viola lanceolata* subspp. *lanceolata* and *vittata* (Greene) Russell (*V. vittata* Greene), both $2n$ = 24; *V. Macloskeyi* F. E. Lloyd subsp. *pallens* (Banks) M. S. Baker (*V. pallens* (Banks) Brainerd), $2n$ = 24; and *V. primulifolia* L. subspp. *primulifolia* and *villosa* (Eaton) Russell (including *V. rugosa* Small), both $2n$ = 24, represent the group in our area. These species seem to intercross freely, and putative natural hybrids of all of them have been recorded. Experimental hybrids between *V. Macloskeyi* subsp. *pallens* and *V. lanceolata*, as well as *V. primulifolia*, have been reported to be fertile.

Subsection *Blandae* Pollard, in part (*Stolonosae* ser. *Blandae* Gershoy, *Incognitae* Clausen), is composed of the closely related *Viola incognita* Brainerd and *V. blanda* Willd., which differ from the preceding white-flowered species in the prostrate peduncles of cleistogamous flowers, the ovoid, purplish or reddish capsules, and the chromosome number ($2n$ = 44). Primarily northeastern, both reach their southern limits in our area. Where the two are in contact "there is morphological intergradation, due to relatively unrestricted intercrossing" (Russell, 1955).

Subsection *Boreali-Americanae* W. Becker, the acaulescent "blue" violets, includes exclusively North American species with fleshy, thickened rhizomes without stolons, blue-to-violet flowers (white in albinic forms), and a common chromosome number ($2n$ = 54). About ten of the twenty-five species recorded from our area are primarily or exclusively southeastern. Others (as *Viola papilionacea* Pursh [including *V. Priceana* Pollard], *V. palmata* L., *V. cucullata* Ait., *V. sagittata* Ait., and *V. fimbriatula* Sm.) are of wide distribution in eastern North America. The species intercross freely, and numerous natural and experimental hybrids, the latter vigorous and usually fertile, are known. Introgression seems to be frequent. At least some of the species probably should be reduced to subspecific rank. This subsection is one of the most difficult groups taxonomically, both because of general morphological similarities and because "frequent hybridization tends to obliterate not only the morphological differences, but also the more sharply marked ecological preferences" (Russell, 1960). Experimental hybrids between subsects. *Primulifoliae* and *Boreali-Americanae*, $2n$ = 39, 51, are sterile.

Subsection *Pedatae* Pollard differs from the preceding primarily in the clavate beakless style, obliquely concave at the summit and bearing the stigma within a small protuberance near the center of the cavity, as well as in chromosome number ($2n$ = 56). The single species, *Viola pedata* L., widely distributed in eastern North America, is considered to be most closely related to *V. Brittoniana* Pollard (*Boreali-Americanae*). The absence of cleistogamous flowers has been regarded as characteristic, but these have been recorded by Hills (1946) in plants cultivated in England.

No natural hybrids are known, and experimental attempts have failed. However, Russell and Bowen concluded (on the basis of vegetative features alone!) that a form with unusual leaf variation in North Carolina was probably the result of hybridization and subsequent introgression between *V. pedata* and *V. primulifolia* subsp. *villosa* (subsect. *Primulifoliae*).

Section VIOLA (§ *Nomimium* Ging., in part; § *Rostellatae* Boiss. sensu Clausen, 1951) includes North American, Eurasian, and North African species of a polyploid series based on ten ($2n$ = 20, 40, (60), 80). Subsection *Uncinatae* Kupff. comprises acaulescent, often stoloniferous violets with the style curved in a hook at the tip and the seeds not forcibly scattered from the capsule. *Viola odorata*, sweet or English violet, $2n$ = 20, has been introduced and has become locally established in various parts of the United States. The North American–Eurasian subsect. *Rosulantes* Borb. includes caulescent blue violets with tufted stems and rosulate basal leaves, rather slender styles beaked and bent at the apex, and seeds forcibly ejected from the capsules. The Eurasian species are diploid or tetraploid, but the North American, with the exception of the western *Viola Howellii* ($2n$ = ca. 80), are diploid. *Viola conspersa* Reichenb., *V. rostrata* Pursh, and *V. striata* Ait., all $2n$ = 20 and linked by partially fertile hybrids, reach their southern limits in our area, while *V. Walteri* House, $2n$ = 20, is primarily southeastern. *Viola adunca* Sm., of more northern distribution, apparently also belongs to this group.

Section MELANIUM Ging. includes about 50 almost exclusively Eurasian and North African species exhibiting a variety of chromosome numbers in a modified six- or ten-series. Only subsect. *Tricolores* W. Becker sensu Clausen (1929) (*Calcaratae*, *Tricolores* W. Becker) including species with chromosome numbers based on x = 6 ($2n$ = 14, 16, 24, 26, 34, 36, 48) is represented in North America. *Viola Rafinesquii* Greene (*V. Kitaibeliana* R. & S. var. *Rafinesquii* (Greene) Fern.), $2n$ = 34, a small annual (or biennial) with bluish-white, creamy, or rarely lavender flowers, occurs from Georgia to Texas and northward beyond our limits. Being distinct from the related European species morphologically and from *V. Kitaibeliana*, $2n$ = 14, 16, 24, 36, 48, especially in the chromosome number, it is also supposedly the only species of sect. MELANIUM which produces cleistogamous flowers (Gershoy, 1934). The nativity of this species in North America has been neither proved nor disproved. *Viola arvensis* Murr., $2n$ = 34, introduced from Europe, has been recorded as naturalized in North Carolina and northward to Newfoundland, Michigan, and Alberta. *Viola tricolor* L., $2n$ = 26, from Eurasia and North Africa, and especially its garden forms of hybrid origin (pansies, "violas," etc.), are commonly cultivated. The *Tricolores* as a group are notable for the occurrence of polyploidy and polysomaty.

The violets, in general, seem to show a preference for acid soil, the degree of acidity varying with each species, although growth of plants "is not correlated with the soil acidity alone, but is influenced by a combination of this factor with moisture, texture, and fertility" (McCullough, 1941). Vegetative reproduction by rooting stolons (e.g., in

Primulifoliae and *Blandae*) or by the detachment of rooting lateral, superficial branches of the rhizome (e.g., in *Boreali-Americanae*), more rarely by adventitious buds on roots (in *Pedatae*), permits the survival of sterile hybrids. Mycorrhiza have been found in *Viola palustris* L. and *V. biflora* L.

Although apparently often self-fertile, the chasmogamous flowers are adapted to cross-fertilization, self-pollination being prevented by the position of the stigma in regard to the anthers, and/or by configuration of the stigma, or by proterandry (*V. lanceolata*, *V. Macloskeyi*). Thysanoptera (especially Thripidae) and various Diptera, Hymenoptera, and Lepidoptera have been recorded as pollinators, the short-tongued species pollinating the short-spurred flowers, the long-tongued the long-spurred violets. These insects usually are in a reverse position (the head down) when sucking the nectar. Details of pollination differ somewhat in different sections. *Viola arvensis* is self-fertilized, and self-pollination occurs early, in the flower buds.

In the great majority of the species of sects. CHAMAEMELANIUM, VIOLA, and PLAGIOSTIGMA, the chasmogamous flowers are followed by reduced, mostly apetalous, closed, highly fertile, cleistogamous flowers with 2–5, ± reduced, spurless stamens and flexuous and much curved styles, so that the stigma is brought into contact with the anthers. The pollen grains germinate within the anthers, and the pollen tubes penetrate the anther walls into the stigma. The presence of dimorphic pollen grains in both chasmogamous and cleistogamous flowers in *V. odorata* var. *praecox* Gregory is noteworthy; only one kind of these pollen grains is germinable in the chasmogamous, and only the other in the cleistogamous, flowers (Madge, 1929). Semicleistogamous flowers forming a transition between chasmo- and cleistogamous flowers are often observed. In many hybrids the sterility involves only the chasmogamous flowers, seeds being produced by the cleistogamous flowers. Apomixis, although presumed by some earlier taxonomists, has not been proved in *Viola*. Myrmecochory has been reported in several species.

Many species are valued ornamentals. Roots of *Viola tricolor* and *V. odorata* contain a saponin and an alkaloid, *violin*, and are official (expectorants) in some countries. A medicinal preparation, *traviolin*, is obtained from the leafy stems of *V. tricolor* in the U.S.S.R. *Viola odorata* is extensively cultivated in Europe for use in perfume manufacturing.

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COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, III
FORM AND DISTRIBUTION OF CRYSTALS IN PERESKIA, PERESKIOPSIS AND QUIABENTIA *

I. W. BAILEY

SINCE THE PUBLICATION of Schleiden's classical paper (1845) on the anatomy of Cactaceae, many references, frequently more or less casual or incidental, have been made to the occurrence of crystals in various representatives of the family. The most comprehensive of these papers is that of Lauterbach (1889) who utilized crystals of calcium oxalate in correlation with mucilaginous and other structures in an attempt to differentiate three categories of the Cactaceae.

Inadequate attention in investigations of cacti has been given to ranges of variability of selected diagnostic characters, not only in different taxa, different collections of the same taxon, and different plants of the same clone, but also in different parts of the same plant during successive stages of its growth to maturity. It seems advisable, accordingly, to determine to what extent crystals provide reliable and significant taxonomic evidence in the case of the leaf-bearing genera of the Cactaceae.

CRYSTALS OF LEAVES

Druses of calcium oxalate occur in the leaves of all putative species of *Pereskia*, *Pereskiopsis*, and *Quiabentia* of which I have succeeded in obtaining material (FIGS. 1–12). This is true, regardless of whether the plants were grown in greenhouses, botanical gardens, or in their native habitats in the wild. The druses vary widely in size, form and number, as they likewise do in the size, form and number of their constituent crystals (FIGS. 13, 15, 16). The conspicuous differences in size (FIG. 1 *vs.* 4), in number (FIG. 3 *vs.* 1 and 4), and in form (FIG. 15 *vs.* 16) suggest at first sight that crystals might be of considerable utility in the differentiation of taxa. Unfortunately, this proves to be uncertain and difficult when the ranges of variability in leaves are taken into consideration. Conspicuous differences such as are illustrated in FIGS. 1–12 may occur at times in different leaves of the same taxon, clone or individual plant. For example, the conspicuous differences between FIG. 7 and FIG. 8 occur in two leaves from the same herbarium specimen. It is evident that differences may occur in leaves during successive stages of their maturation, in

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leaves of different sizes, in leaves of plants of different ages, and in those of plants grown under differing environmental conditions. Therefore, the task of securing strictly comparable material of different taxa becomes a difficult and extremely laborious one.

Although a majority of the crystals of calcium oxalate in the leaves of these genera occur in the form of druses having radially oriented individual crystals of varying forms and sizes, aberrant types of crystallization are of not infrequent occurrence.

Particularly where the crystals are very abundant (FIG. 3), some of the cells of the mesophyll may contain a single crystal, several independent crystals or aggregations of crystals that are not perfectly oriented radially.

CRYSTALS OF CORTEX AND PITH

Druses of conspicuously stellate (FIGS. 13, 15) or more rotund (FIGS. 14, 16) form occur in the pith and cortex of all three genera of the leaf-bearing Cactaceae. The size, form, and number of the druses is highly variable, as in the case of the leaf. One or more independent crystals of varying size and form may occur at times in some of the cells of the pith and cortex. It is possibly significant taxonomically that there appears to be marked exaggeration of this tendency in the much expanded pith of large basal stems of *Pereskia conzattii* Britt. & Rose (FIG. 17) and in the cortex of large older stems of *Pereskia colombiana* Britt. & Rose and *P. guamacho* Web.

The most constant and reliable difference, and one of considerable phylogenetic and taxonomic significance, is the concentration of rotund forms of druses in the outermost layer of the cortex of *Pereskiopsis* and *Quiabentia*. In the case of *Pereskia sacharosa* Griseb., *P. grandifolia* Haw., *P. bleo* DC., *P. corrugata* Cutak, *P. tampicana* Web., and allied taxa, young stems of varying diameter, before periderm formation, have a thick cuticle (FIG. 25). The cells of the cortex decrease in size toward the epidermis. Although their cell walls increase somewhat in thickness toward the exterior of the cortex, no clearly differentiated collenchymatous layers are formed subtending the epidermis. The druses are diffusely distributed in the cortex (FIG. 25). In comparable stems of *Pereskiopsis* and *Quiabentia* conspicuous layers of subepidermal collenchyma are formed (FIG. 27). The outermost layer of the collenchymatous zone is packed with druses of rotund, rather than conspicuously stellate, form (FIGS. 19, 23, 26). The larger druse-bearing cells tend to bulge the relatively tenuous cuticle and slender epidermal cells outward (FIG. 27). Apparently with increasing succulence in *Pereskiopsis* and *Quiabentia* the inner cells of the cortex tend to become thinner walled, whereas the outer ones become thicker walled and collenchymatous. The first cork cambium or phellogen usually arises by periclinal divisions of epidermal cells and the periderm intervenes between the remainder of the epidermis and the outermost layer of crystal-bearing collenchyma. Thus, the latter layer persists after

periderm formation has occurred and may be detected for some time in older stems.

In the case of *Pereskia aculeata* Mill., *P. colombiana*, *P. guamacho*, *P. cubensis* Britt. & Rose, *P. portulacifolia* Haw., *P. diaz-romeroana* Cárd., *P. weberiana* K. Schum., *P. conzattii*, *P. autumnalis* (Eichlam) Rose, and *P. nicoyana* Web., periderm formation commonly tends to be precocious and the epidermis and the outer layers of the cortex are rapidly modified. Although the stems of these pereskias do not form such clearly and strongly differentiated collenchymatous layers as occur characteristically in *Pereskiopsis* and *Quiabentia*, they do exhibit at times a tendency for the outer cortical cells to have thicker walls. Particularly in *P. diaz-romeroana* and *P. weberiana* some druses of rotund form may occur in the outermost cells of the cortex. This suggests that in these species there may be a tendency toward structural changes such as become exaggerated and dominant in *Quiabentia* and *Pereskiopsis*.

In view of the occurrence of so-called crystalliferous hypodermal layers in other cacti, the phenomenon merits detailed consideration in subsequent discussion of salient trends of phylogenetic specialization in the Cactaceae as a whole.

CRYSTALS OF THE SECONDARY PHLOEM AND XYLEM

Druses of varying degrees of abundance occur in the secondary phloem of the three leaf-bearing genera. Although usually of spherical form, they may at times exhibit curious deviations in elongated parenchymatous elements (FIG. 21). In such cells the druses may have a markedly elongated form and have conspicuously larger crystals at their upper and lower extremities (FIG. 18).

As in the case of the leaf, pith and cortex, cells having one or more independent crystals are of sporadic occurrence. However, it is again noteworthy in this connection that in large stems of *P. colombiana* and *P. guamacho* cells with single crystals may predominate in the older secondary phloem, druses being relatively infrequent in comparison.

Pronounced differences in forms of crystallization of calcium oxalate occur in the rays of the secondary xylem. Where the rays are composed of cells having thick, strongly lignified walls, as in many pereskias, crystals either are absent or, when present, occur in a cell singly (FIG. 22) or as several independent crystals, druses being absent. On the contrary, where the rays or parts of them are composed of thin, unlignified cells, a varying number of the thin-walled cells form druses (FIG. 20). It is significant in this connection from a phylogenetic point of view that changes in the rays and forms of crystallization within them appear to be associated in some way with tendencies toward increasing succulence of stems and roots This is another phenomenon which deserves detailed consideration in subsequent discussion of salient trends of phylogenetic specialization in the Cactaceae as a whole.

SPHEROCRYSTALS AND STRIATED ISOTROPIC BODIES

Möbius (1885) early recorded the occurrence of spherocrystals of calcium oxalate in Cactaceae. His illustrations of the structural features of these crystalline bodies are reproduced by Kohl (1889), and two of them by Solereder (1899) and by Metcalfe and Chalk (1950).

A few finely striated bodies that are birefringent in polarized light occur sporadically in some of my collections of leaf-bearing cacti that are preserved in formalin-acetic-alcohol. Where they occur in small cells, and in one case in the lumen of vessels close to the cambium, they tend to be fan-shaped or hemispherical in surface view, rather than spherical as in large-celled tissue (FIG. 29). Where a cluster of cells contains them, the striations of each body are radially oriented toward the center of the aggregation of cells. In the case of the larger spherical forms, not only are they radially striated, but also at times they exhibit concentric structure as well, thus resembling certain of the spherocrystals illustrated by Möbius. They also show at least superficial resemblances to the finely striated central parts of some of the more rotund forms of druses (FIG. 16).

Furthermore, particularly in the case of the crystalliferous subepidermal layer of *Pereskiopsis*, the druses not only exhibit a radially striated central part (FIG. 23) but also not infrequently are concentrically layered internally (FIG. 28). Such rotund forms of druses differ from the spherocrystals (FIG. 29) in being jacketed by a layer of large, more or less protuberant crystals. This raises a question in need of detailed investigation. Are there transitional forms of crystallization of calcium oxalate between typical stellate druses and structures commonly referred to as spherocrystals? Or are there fundamental differences in chemical composition involved?

In contrast to these relatively infrequently occurring anisotropic bodies are the dark brown, striated, isotropic ones commonly visible during early stages of the clearing of dried leaves in 3 per cent sodium hydroxide at 56° C., i.e., prior to their bleaching and dissolution. Although these bodies vary greatly in size and form, they tend to be more or less conspicuously striated. Some of them exhibit concentricities as well as radial striations (FIG. 30), thus in surface view resembling spherocrystals (FIG. 29). Others are composed of small cells the brown contents of which have striations oriented radially toward the center of the composite mass (FIG. 32). Where the constituent cells of the mass are larger, the radial orientation of the striations is more clearly visible (FIG. 33). In surface view such a mass of isotropic composition bears at least a superficial resemblance to Möbius' figures 10–13 of spherocrystals. Under more prolonged treatment in sodium hydroxide brown structureless globules frequently tend to exude from the striated bodies (FIG. 31), or the whole body may lose its striated structure. Obviously, such bodies are not composed of crystalline calcium oxalate, although they occasionally may contain some in the form of "crystal sand." It should be emphasized in these connections that the brown bodies in dried leaves differ from the sphero-

crystals dealt with by Möbius (1885), Kohl (1889), Lauterbach (1889), and Michaëlis (1896) in being isotropic rather than birefringent in polarized light.

It is important to determine not only the chemical and physical constitution of crystalline and isotropic bodies that occur in material of cacti, but also to obtain reliable evidence regarding the occurrence of such bodies in normal living tissue prior to desiccation, preservation in alcohol or formalin-acetic-alcohol and subsequent treatments with varying reagents. At present, there is adequate evidence regarding the common occurrence of druses of calcium oxalate in normal unmodified tissues of various Cactaceae, as well as in the leaf-bearing ones. However, there is evidence which indicates that the druses are not composed solely of calcium oxalate, but contain organic substances as well, particularly in their central parts. For example, when druses are treated with haematoxylin prior to the use of reagents which dissolve constituents such as residues of nuclei, protoplasts, etc., their centers stain very dark (FIGS. 14, 19, 20, 23). Furthermore, if the calcium oxalate is dissolved prior to such treatment, a deeply stained central part of the druse persists. (Compare FIGS. 23 and 24.)

The spherocrystals studied by Möbius are stated to occur, at least in certain cases in living tissue, whereas those observed by Lauterbach and Michaëlis occurred in material preserved in alcohol The formation of dark brown isotropic bodies in the leaves of *Pereskia*, *Pereskiopsis*, and *Quiabentia* appear to be induced by desiccation or other modifying treatments. However, their formation in all three genera is indicative of the presence of similar organic substances and may ultimately prove to be of some taxonomic significance in comparisons between the leaves of Cactaceae and those of other families of the dictotyledons, e.g., those included in the Centrospermae. Thus, their chemical composition and factors involved in their formation merit detailed investigation.

CONCLUSIONS

The ranges of variability in the size, form, and number of druses in the leaves of *Pereskia*, *Pereskiopsis*, and *Quiabentia* are so extensive as to render their use difficult and excessively laborious in differentiating the three genera and the species which occur within them.

The most constant and reliable differences from phylogenetic and taxonomic points of view are those that occur in the outer cortex of young stems prior to periderm formation. *Pereskiopsis* and *Quiabentia*, in contrast to *Pereskia*, have conspicuous collenchymatous layers, the outermost of which is packed with druses of rotund form subtending the epidermis.

Another difference of considerable phylogenetic and physiological interest occurs in the rays of the secondary xylem of both stems and roots. Where the rays are composed throughout of cells with thick, heavily lignified walls, as in less modified forms of woody dicotyledons, deposition of calcium oxalate occurs in the form of single crystals or several independent ones, aggregation into druses being absent or of rare occur-

rence. On the contrary, where the rays or parts of them are composed of cells with thin unlignified walls, such rays or parts contain more or less numerous druses. The changes in wall thickness, lignification and form of crystallization appear to be correlated in some manner with tendencies toward increasing succulence, as in *Pereskiopsis* and *Quiabentia*.

The changes in the outer cortex of *Pereskiopsis* and *Quiabentia* and in the rays of the leaf-bearing cacti appear to be significant in any subsequent discussion of salient trends of phylogenetic specialization in the Cactaceae as a whole.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–6. Parts of leaves cleared in 3 per cent sodium hydroxide at 56°C., dehydrated, and mounted in diaphane. Druses photographed in polarized light between crossed nicols at a magnification of 150. 1, *Quiabentia zehntneri* (Britt. & Rose) Britt. & Rose [*Rose*, N.Y. Bot. Gard. 42830]; 2, *Pereskiopsis gatesii* Baxter [Gates Cactus Inc.]; 3, *Pereskiopsis diguetii* Britt. & Rose [*Safford*, U.S. Nat. Herb. 2263439]; 4, *Pereskia bleo* DC. [*Pennell 4759* (GH)]; 5, *Pereskia portulacifolia* [*Jiménez 2578* (US)]; 6, *Pereskia aculeata* [*Duss 3073* (GH)].

PLATE II

FIGS. 7–12. Parts of leaves cleared in 3 per cent sodium hydroxide at 56°C., dehydrated, and mounted in diaphane. Druses photographed in polarized light between crossed nicols at a magnification of 150. 7, *Pereskia* aff. *guamacho* [*H. H. Smith 1886* (GH)]; 8, Another leaf from *Smith 1886*; 9, *Pereskia grandifolia* [*Mexia 4129* (GH)]; 10, *Pereskia grandifolia* [*Moran 7270*]; 11, *Pereskia conzattii* [*Boke*]; 12, *Pereskia nicoyana* [Mo. Bot. Gard.].

PLATE III

FIGS. 13–18. Druses photographed in green light at a magnification of 425. 13, *Pereskia diaz-romeroana* [*Cárdenas*], stellate druse from leaf; 14, *Pereskia tampicana* [*Boke B-17*], druse from cortex of stem; 15, *Pereskia* aff. *guamacho* [*Smith 1886* (GH)], stellate druse from leaf; 16, *Pereskia grandifolia* [*Mexia 4129* (GH)], druse from leaf; 17, *Pereskia conzattii* [*Dressler*], crystals from pith of large basal stem; 18, *Pereskiopsis chapistle* Britt. & Rose [*Boke B-3*], druse from phloem parenchyma.

PLATE IV

FIGS. 19–24. Varied forms of crystals in stems. 19, *Pereskiopsis chapistle* [Mo. Bot. Gard.], tangential longitudinal section stained in haematoxylin and Sudan III and mounted in glycerin, showing druses in outer layer of collenchyma subtending the epidermis, as seen in polarized light, × 150; 20, *Pereskiopsis chapistle* [*Boke B-3*], tangential longitudinal section of xylem stained in haematoxylin and safranin and mounted in diaphane, showing stellate druses in thin-walled, unlignified ray parenchyma as seen in polarized light, × 150; 21, *Pereskiopsis chapistle* [*Boke B-3*], tangential longtitudinal section of phloem, showing druses in elongated parenchymatous elements, as seen in polarized light, × 150; 22, *Pereskia colombiana* Britt. & Rose [*Romero*], tangential longitudinal section of xylem showing single crystals in thick-walled lignified ray cells, in polarized light, × 150; 23, *Pereskiopsis chapistle* [Mo. Bot. Gard.], single druse from Fig. 19 photographed in green light, × 425; 24, *Pereskiopsis scandens* Britt. & Rose [N.Y. Bot. Gard. 50085], organic residues of such a druse as illustrated in Fig. 23 after removing the crystals of calcium oxalate in a mixture of equal parts of 10 per cent nitric and 10 per cent chromic acids, staining in haematoxylin and safranin and mounting in glycerin, photographed in green light, × 425.

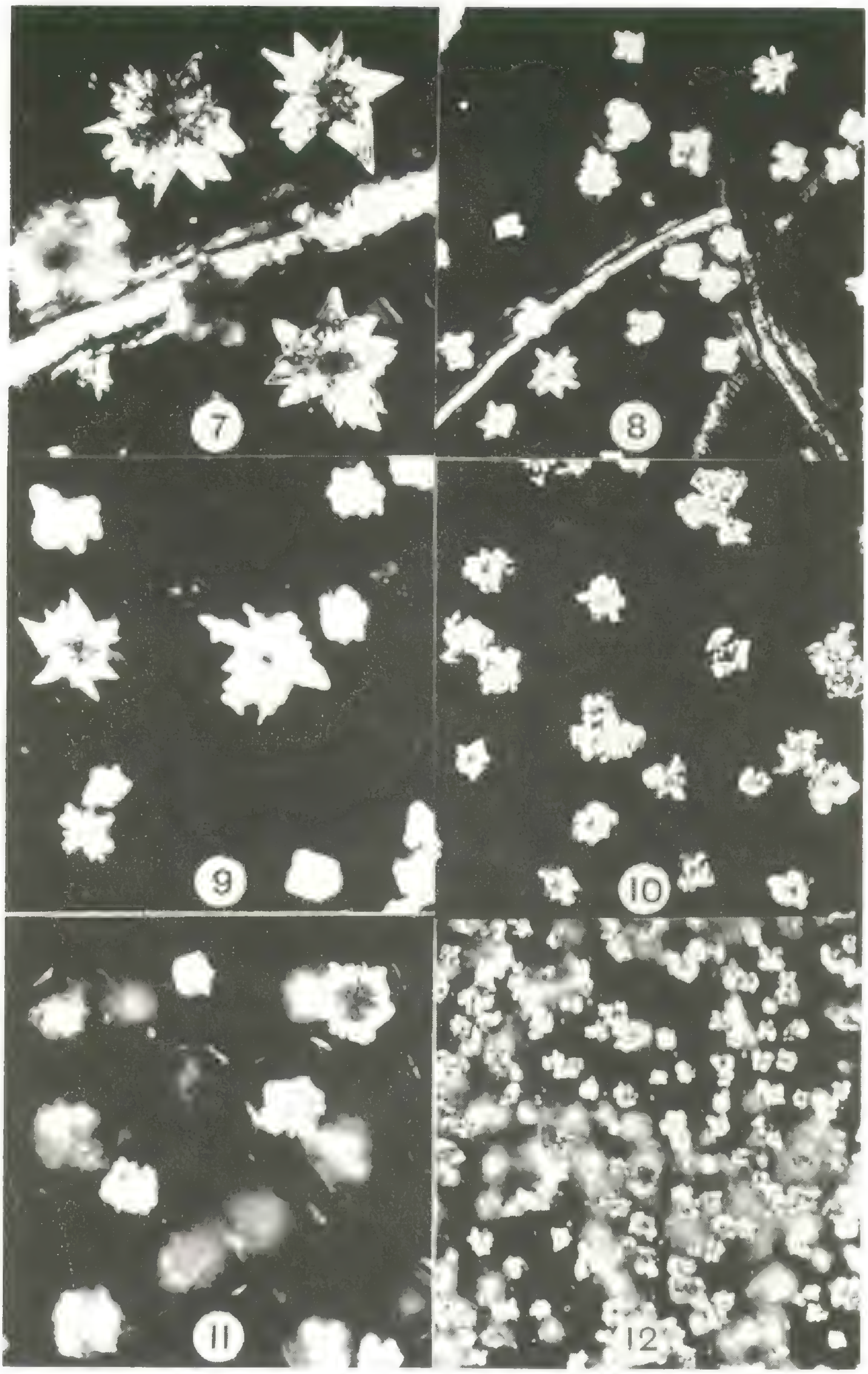
PLATE V

FIGS. 25–27. Transverse sections of stems. 25, *Pereskia sacharosa* [Mo. Bot. Gard.], stained with haematoxylin and safranin, mounted in diaphane, showing thick cuticle, conspicuous epidermis and diffuse distribution of druses in cortex, photographed in green light, × 150; 26, *Pereskiopsis scandens* Britt. & Rose [N.Y. Bot. Gard. 50085], unstained section mounted in diaphane and photographed in polarized light, showing concentration of druses in subepidermal layer of outer collenchyma, × 150; 27, *The same*, section stained in haematoxylin and safranin, mounted in diaphane and photographed in green light, showing collenchymatous layers in contrast to Fig. 25, and tenuous epidermis bulging outward owing to the development of druses shown in Fig. 26, × 150.

PLATE VI

FIGS. 28–33. Crystalline and isotropic bodies in green light; Fig. 28, × 1000; Fig. 29, × 500; Figs. 30–33, × 260. 28, *Pereskiopsis aquosa* (Web.) Britt. & Rose [N.Y. Bot. Gard.], concentrically layered druse; 29, *Pereskia guamacho* [Atkins Gard.], anisotropic "sphaerocrystal" from pith; 30, *Pereskia* aff. *guamacho* [*Smith 1886* (GH)], brown, radially striated, concentrically layered, isotropic mass, foliar; 31, *Pereskia aculeata* [*Ferreira 2316* (GH)], exudation of structureless brown droplets from radially striated, isotropic mass, foliar; 32, *Pereskia grandifolia* [*Moran 7270*], mass of small cells with striated, brown, isotropic contents, foliar; 33, *Pereskia colombiana* [*Record 16495* (GH)], mass of large cells with striated, brown, isotropic contents, foliar.

BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, III



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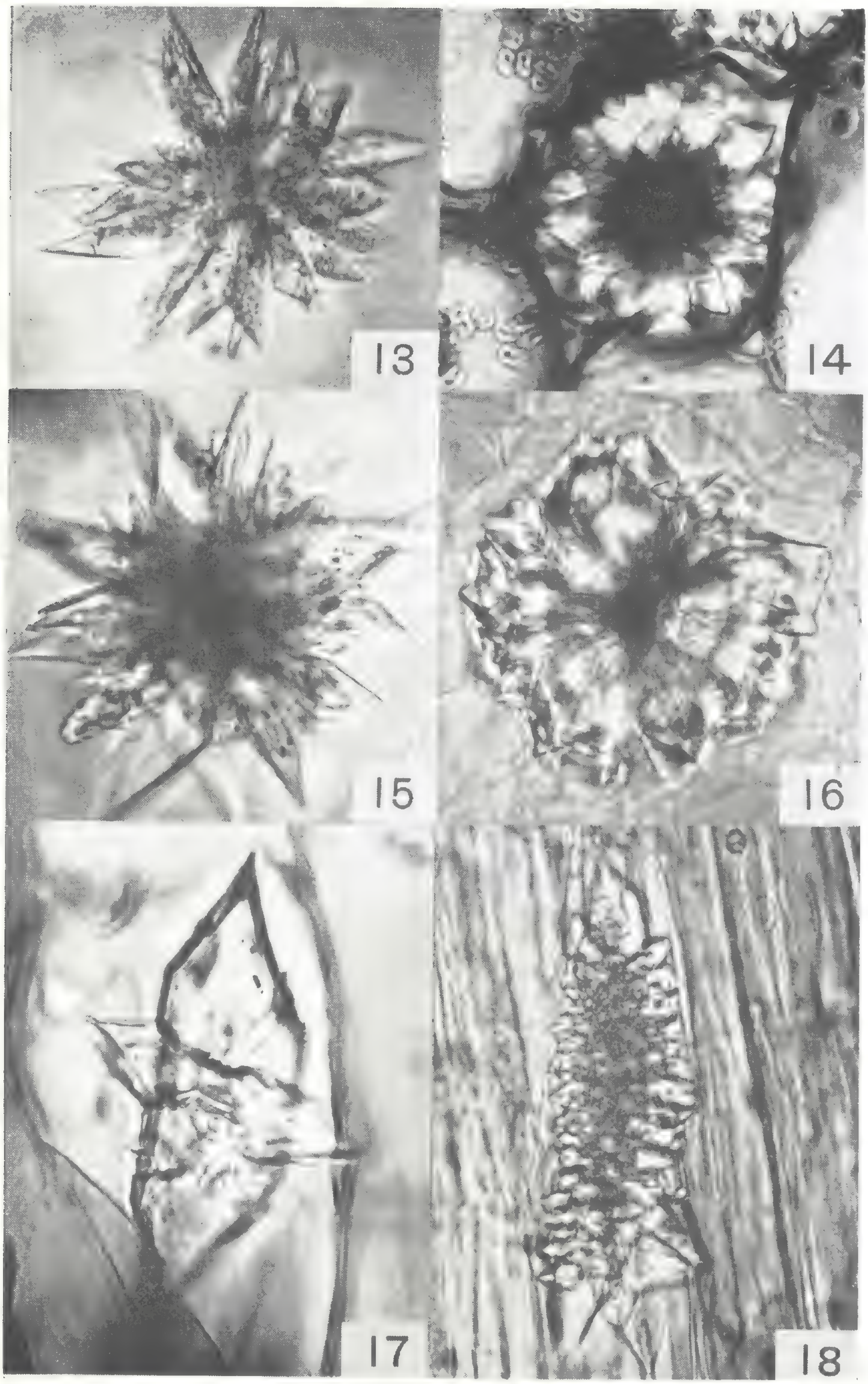

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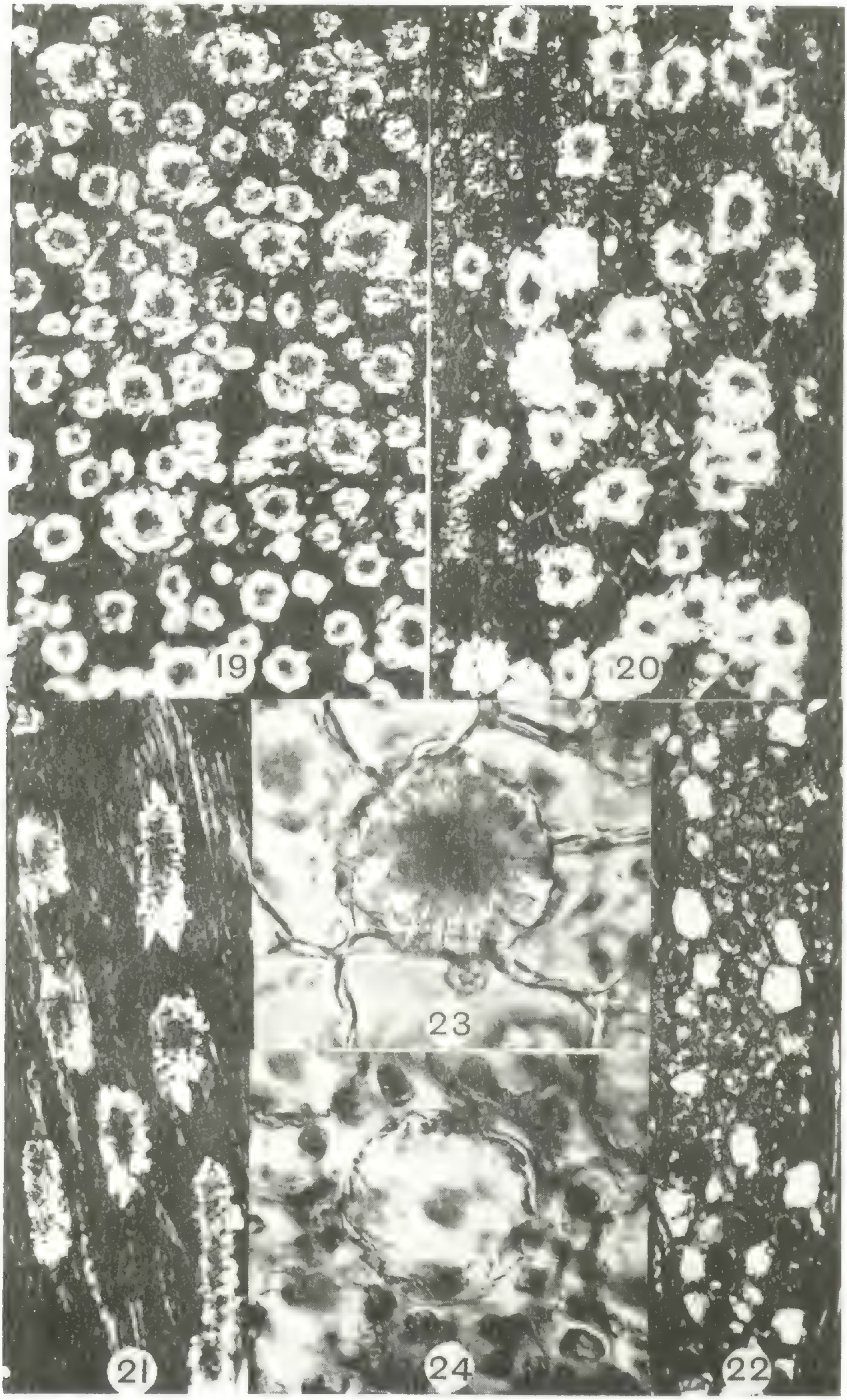

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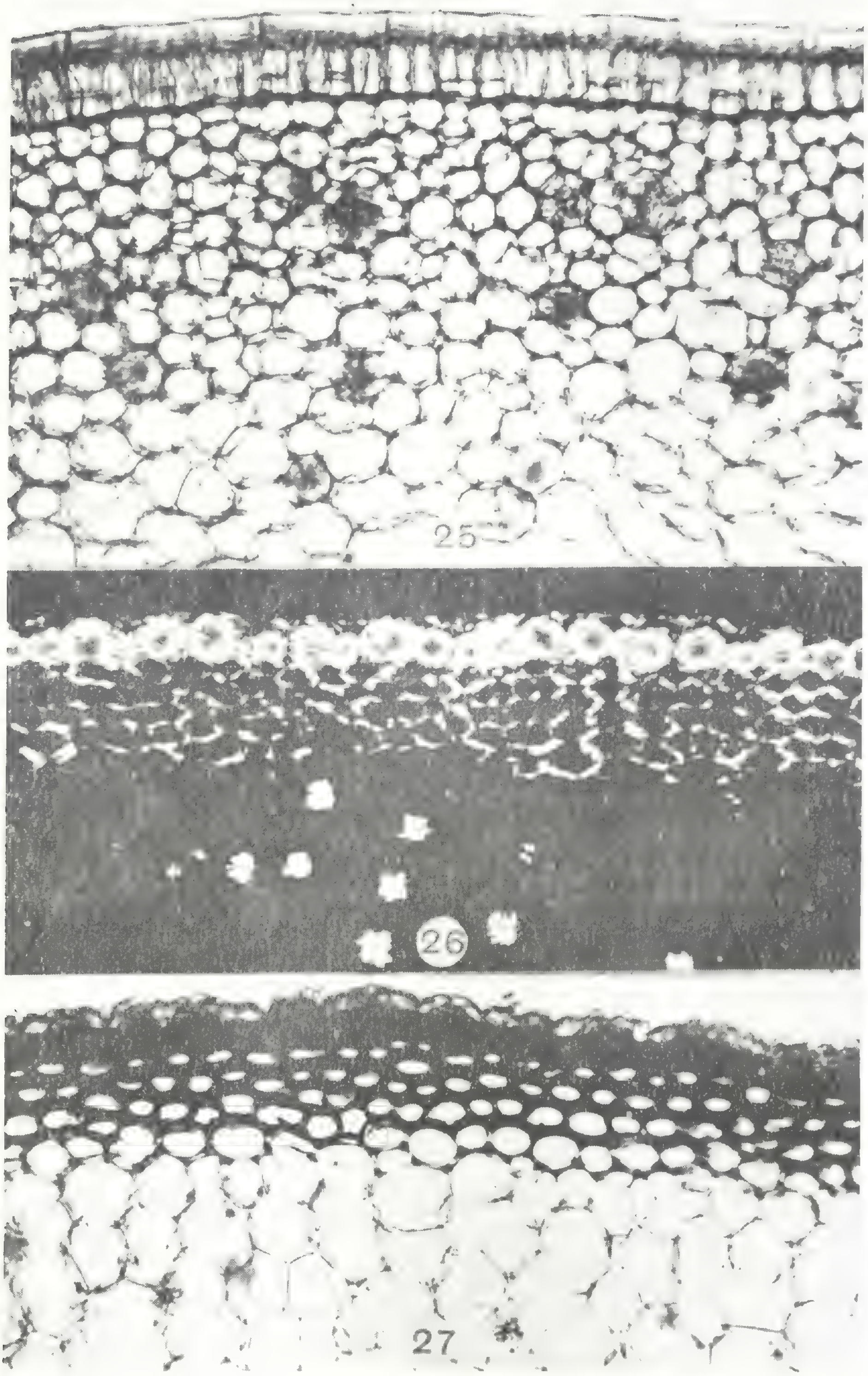

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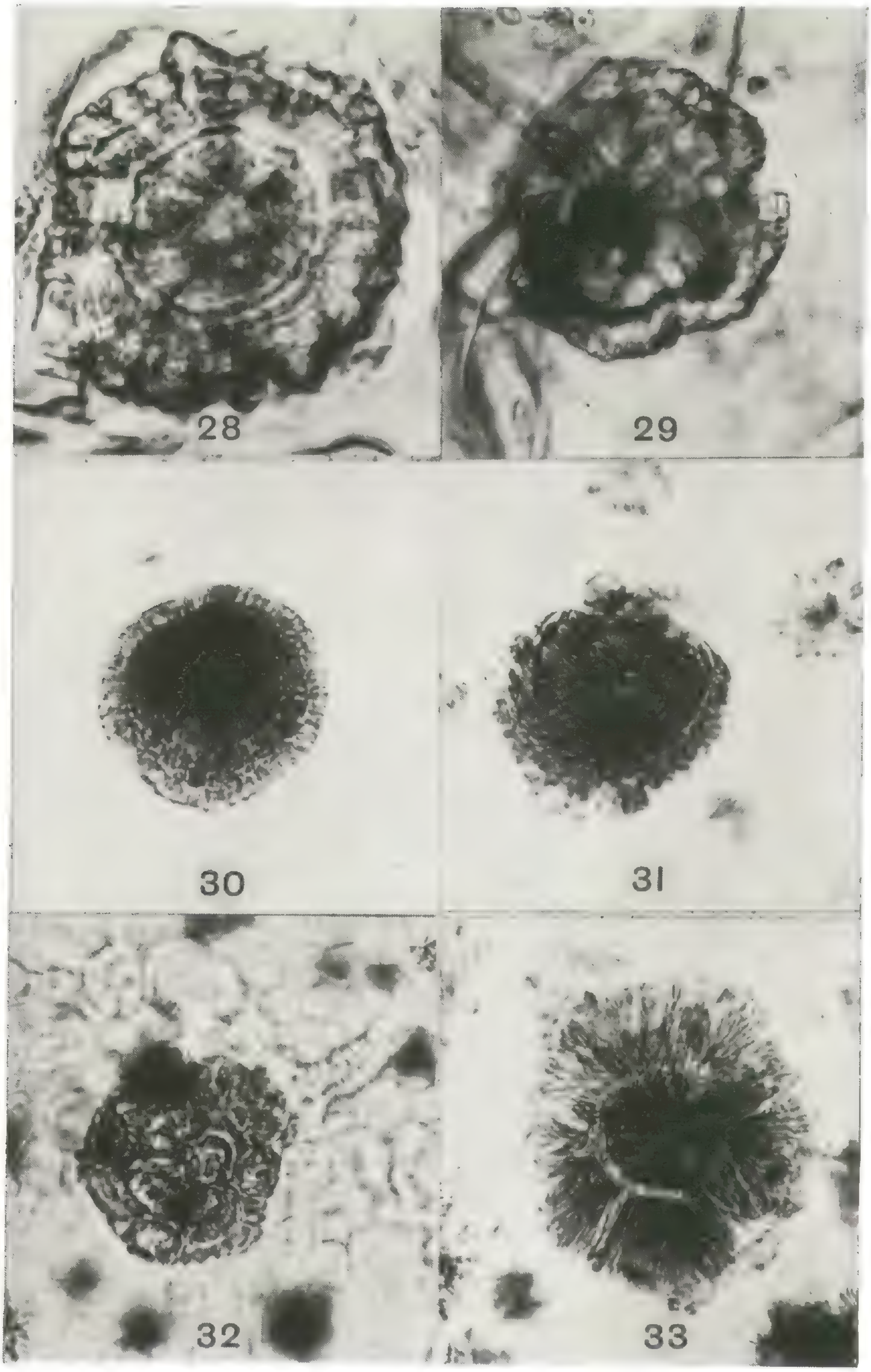

BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, III

MIOCENE FOSSIL WOODS FROM THE COLUMBIA BASALTS OF CENTRAL WASHINGTON, II

U. Prakash and Elso S. Barghoorn

In a previous paper (1961) the authors described in detail twelve species of woods, representing nine genera (*Acer*, *Diospyros*, *Quercus*, *Liquidambar*, *Carya*, *Albizzia*, *Gleditsia*, *Platanus*, and *Ulmus*) from the Columbia Basalts of the area of Vantage, Washington. The silicified woods described represent a small fraction of an extensive collection made in 1954 by Mr. Jay O'Leary, while he was a student in Harvard College. The present investigation is a continuation of the systematic study of this collection. In this paper we are concerned with the identification and description of six additional species representing four genera not recorded in the first paper. It is probable that the total number of genera preserved in the basalts of the Vantage area may be in excess of 30 of which more than two-thirds are genera of dicotyledonous trees. In a previous communication, Beck (1945) listed 27 genera determinable in the Vantage and nearby stratigraphically equivalent areas. It is of interest to note that only slightly more than one-third of these genera currently exist in the flora of the general region today (Wolfe and Barghoorn, 1960).

Although the age of the flora with which our study is concerned is generally regarded to be Upper Miocene, the high percentage of genera represented in this fossil flora but now exotic to the region would tend to indicate a lower stratigraphic position in the Miocene sequence (Barghoorn, 1951; Wolfe and Barghoorn, 1960). This reconsideration of the age of the Vantage (Russell Forests) flora is also supported by comparison of generic composition with that of the Latah flora, a large flora the composition of which is known from leaf impressions rather than silicified woods. The Latah flora is comprised of genera of which only slightly more than one-third are extant in the geographic region today. Statistical examination of thirteen floras of the western United States generally regarded as Upper or Late Miocene, on the other hand, indicates that between 50 to 67 per cent of their genera are yet in the geographic region of the fossil floras.

FAGACEAE

1. **Quercus sahnii** Prakash & Barghoorn, sp. nov. (Figs. 16–19)

Growth rings: Distinct; wood ring-porous. Transition between early and late wood abrupt. (Fig. 19).

Vessels: Large vessels in the early wood (Fig. 19), 192–416 μ in tangential diameter (mean diameter 269 μ), solitary, forming a conspicuous band 1 or 2 pores in width, thin walled, vessels round to oval, occasionally

elliptical in cross-section. Vessel elements 240–540 μ long. Perforation plates exclusively simple, usually horizontal. Intervascular pit-pairs alternate, bordered and round to oval in shape. Tyloses absent. Late-wood vessels small (FIG. 19), 30–111 μ in tangential diameter (mean diameter 70 μ), usually scattered in radially aligned, flame-shaped tracts of light-colored tissue, chiefly solitary, open, thick walled (FIG. 17), rounded in cross section. Perforation plates and intervascular pit-pairs similar to early wood vessels.

Parenchyma: Abundant, paratracheal, metatracheal-diffuse, and metatracheal. Paratracheal parenchyma intermingled with the tracheids, (1) forming part of the conjunctive tissue between the early wood vessels and the rays, (2) composing most of the tissue in the flame-shaped tracts in which late wood vessels are embedded. Metatracheal-diffuse parenchyma (FIGS. 17, 19) restricted to fibrous tracts and exhibiting a tendency towards aggregation into short, irregular lines of metatracheal parenchyma towards the outer part of the ring. Crystalliferous parenchyma frequent, composed of somewhat enlarged cells containing single crystals (FIG. 18).

Xylem rays: Homogeneous (Kribs Homogeneous Type 1), composed of procumbent cells; both narrow and broad (FIG. 16); narrow rays very numerous, uniseriate, 2–27 cells high; broad rays 15–28 cells wide and very high, separated by numerous narrow rays (FIG. 16) often dissected into smaller units. Ray cells oval to polygonal in tangential section and 10–30 μ in diameter, sometimes with crystals.

Imperforate tracheary elements: Libriform fibers and vasicentric tracheids. Thick-walled fibers (FIGS. 17, 19) well developed through the spaces among the flame-shaped tracts of late wood vessels, polygonal in cross section, 12–21 μ in diameter, nonseptate; pits simple. Vasicentric tracheids intermingled with parenchyma, (1) composing most of the conjunctive tissue between the early-wood vessels and the rays and (2) forming part of the flame-shaped tracts in which late-wood vessels are embedded; pits bordered.

MATERIAL. A single specimen of silicified, mature, secondary xylem measuring 6.5 $\times$ 2.5 $\times$ 7 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 54968. This species is named in commemoration of the late Professor Birbal Sahni, founder-director of the Institute of Palaeobotany, Lucknow, India.

There is close agreement in all details of structure of this wood with that of *Quercus*. Among the different types of oaks, the fossil wood belongs to the red-oak group as indicated by the presence of thick-walled, rounded vessels in the late wood. A survey of the available woods of *Quercus* indicates that the fossil does not show close resemblance to any of the species represented in the wood collections of the Arnold Arboretum (86 species) nor to published descriptions of 15 other species (Sudworth & Mell, 1911, pp. *22–56, figs. 11–48*; Kanehira, 1921a, pp. 67–71, *Pl. 8, figs. 44, 45*; Kanehira, 1924, p. 52; Kanehira, 1940; Pearson & Brown, 1932, pp. 981–996, *figs. 299–304*; Reyes, 1938, pp. 60–62, *Pl. 4, figs. 1, 2*;

Metcalfe & Chalk, 1950, pp. 1311–1314, *figs. 313G, L*; Greguss, 1947, pp. 41–46, *figs. 18–27*).

Fossil woods assigned to *Quercus* have been listed by Edwards (1931) and Boeshore and Jump (1938) and were also referred to in our previous paper (Prakash & Barghoorn, 1961). More than 500 species and varieties of *Quercus*, ranging from low shrubs to stately forest trees, are known. There are about 50 species of *Quercus* native to the United States. The species belonging to the red-black oak group are widely distributed almost throughout this country. Those growing in the western United States are *Q. Kelloggii* Newb., of the mountain ranges of California and western Oregon, *Q. tomentella* Engelm., on the islands along the coast of southern California and Guadeloupe Island and extending farther south in Mexico, *Q. douglasii* Hook. and Arn., a tree of wide range in California, and varieties of *Q. dumosa* Nutt., on the coastal islands of southern California and Mexico (Little, 1953). Species of the red-black group of the genus are not known from the state of Washington.

HIPPOCASTANACEAE

2. **Aesculus hankinsii** Prakash & Barghoorn, sp. nov. (Figs. 20–23)

Growth rings: Barely distinct; wood diffuse-porous (Fig. 22).

Vessels: Small, 35–80 μ in tangential diameter (mean diameter 54 μ), more crowded in the early spring-wood, decreasing slightly in size through the late wood, where they are fewer and quite apart (Fig. 22). Vessels solitary and in radial multiples of 2–5 (mostly 2 or 3) cells, thin walled, the solitary vessels oval-angular to elliptical-angular in cross section. Vessel elements up to 500 μ long with oblique, often tailed ends; spiral thickenings occasionally present. Perforation plates exclusively simple. Intervascular pit-pairs (Fig. 21) bordered, alternate, orbicular to oval or angular where crowded, 5–7 μ in diameter, apertures oval to slitlike, sometimes oblique. Vessels open.

Parenchyma: Appearing to be terminal and paratracheal. Terminal parenchyma forming a continuous or interrupted line. Paratracheal parenchyma quite scanty.

Xylem rays: Homogeneous, composed of procumbent cells (Fig. 23), uniseriate, 2–32 (mostly 8–15) cells high, showing a tendency for storied arrangement; up to 16–20 rays per mm. Ray cells thin-walled, oval to vertically elongated in tangential section.

Imperforate tracheary elements: Fiber tracheids rectangular to polygonal in cross section (Fig. 20), 12–23 μ in diameter, walls thin to slightly thick; nonseptate; pits bordered.

Material. A single specimen of silicified, mature, secondary xylem measuring 8 $\times$ 2 $\times$ 6 cm. Preservation poor.

Holotype. Palaeobotanical Collections, Harvard University, No. 56240. The species is named after Mr. Frank W. Hankins, of Collegeville, Pennsylvania, who kindly gave us the fossil wood for study.

The combination of structural features exhibited by this wood indicates its affinity with the genus *Aesculus* and its nearest affinity with the extant species *Aesculus pavia* L. Thin sections of the woods of eighteen species of the genus *Aesculus* were examined in the course of identification, including Asiatic and European, as well as North American, representatives of the genus. The fossil under consideration differs from *A. pavia* in only minor details, the most conspicuous of which are the less frequent occurrence of vessel multiples throughout the growth ring and greater crowding or compaction of vessels in the early wood.

Aesculus hankinsii, as far as the authors are aware, represents the first record of this genus occurring in the form of fossil wood. Its identification supports the conclusions of Beck (1945) on the presence of *Aesculus* in the Vantage and adjacent areas. The genus, as presently constituted, includes thirteen species of trees and shrubs of temperate regions, occurring in southeastern Europe, India to Japan, and North America (Hardin, 1957). *Aesculus pavia* is a shrub, sometimes attaining the dimensions of a small tree, occurring in woods and along streams from eastern North Carolina to Florida, westward to the Edwards Plateau of Texas, and north in the Mississippi Valley to southern Illinois. In present geographic distribution the nearest species is *A. californica* (Spach) Nutt., a small tree of the California Coast Ranges and Sierra Nevada foothills (Hardin, 1957).

JUGLANDACEAE

3. **Juglans fryxellii** Prakash & Barghoorn, sp. nov. (FIGS. 12–15)

Growth rings: Distinct, delineated by narrow band of thick-walled, flattened fibers; wood diffuse-porous to semi-ring-porous (FIGS. 13, 14).

Vessels: Large in early wood, gradually decreasing in size through the late wood with a marked tendency toward diagonal arrangement (FIGS. 13, 14), 51–208 μ in tangential diameter (mean diameter 142 μ), chiefly solitary, sometimes in radial groups of 2 or 3 cells, evenly distributed and closely placed, thin walled, the solitary vessels oval, elliptical, or sometimes slightly irregular in cross section (probably due to pressure during mineralization). Vessel elements of varying lengths, with oblique end walls. Perforation plates not ascertainable, the vessels mostly being plugged with gummy or resinous deposits (FIG. 13). Intervascular pit-pairs (FIG. 12) bordered, alternate, or slightly irregular, 10–14 μ in diameter, usually angular where crowded, pit apertures oval to linear.

Parenchyma: Metatracheal and terminal. Metatracheal parenchyma (FIGS. 13, 14) in uniseriate (rarely locally biseriate), somewhat wavering and more or less parallel tangential lines which are almost always continuous, sometimes small and broken. Terminal parenchyma uniseriate and continuous. Parenchyma cells sometimes enlarged and crystalliferous, usually with black, resiniferous substance.

Xylem rays: Homogeneous to decidedly heterogeneous, 1–3 cells wide (FIG. 15); uniseriate rays few, 2–11 cells high; multiseriate rays mostly

2 or 3 cells broad and 0.56 mm. high; multiseriate rays mostly heterogeneous, sometimes homogeneous and composed of procumbent cells; multiseriate heterogenous rays with procumbent cells in the broad central part and one to several rows of upright cells at the uniseriate ends; end-to-end ray fusion sometimes present; up to 7–12 rays per mm. Ray cells thin walled, oval to vertically elongate in tangential section, 10–15 μ in diameter.

Imperforate tracheary elements: Fiber tracheids, polygonal to slightly irregular in cross section (FIG. 13), 12–22 μ in diameter, the walls slightly thickened; nonseptate; pits bordered.

MATERIAL. Few, small specimens of silicified, mature, secondary xylem.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55045. This species is named after Mr. Roald Fryxell, Curator, Ginkgo Petrified Forest Museum, Vantage, Washington.

The combination of structural features of the fossil, after extensive comparison with modern woods, indicates its affinity with the genus *Juglans*. Among the 15 species of this genus available for direct comparison, the closest approximation in structure is to be found in *Juglans nigra* L. and *J.* × *notha* Rehder, to both of which the fossil wood shows a close resemblance, with only some differences in details of ray structure and parenchyma distribution. One other conspicuous feature of the fossil is the presence in the vessels of a brownish-black substance plugging the vessel lumina.

Fossil woods assigned to the family Juglandaceae are known from a wide range of localities in the Northern Hemisphere, in both Old and New Worlds. The genera have been designated as *Juglandinium* Unger (1845), *Juglandoxylon* Kraus (1882), *Jugloxylon* Stopes & Fujii (1910), *Juglans*, *Pterocarya*, and *Carya*. Species described are *Juglandinium longiradiatum* Vater (Kaiser, 1890), from the Lower Senonian of Germany; *J. mediterraneum* Unger (Kaiser, 1890), and *J. schenkii* Felix (Kaiser, 1890), both from the Tertiary of Hungary; *J. triebelii* (Caspary) Nagel (1915), from the (?) Tertiary of Prussia; *J. wichmannii* (Hofmann) Kaiser (1890), and *J. zuriense* (Falqui) Edwards (1931), from the Miocene of Sardinia; *Juglandinium* spp. (Kaiser, 1890; Schönfeld, 1930; Edwards, 1931), from the Lower Senonian of Brunswick, Upper Cretaceous of western Canada, and the Oligocene of Saxony; *Jugloxylon homanum* Stopes & Fujii (1910), from the Upper Cretaceous of Japan; *Juglandoxylon princeps* (Ludw.) Müller-Stoll (1938) and *J. schadleri* Hofmann (1952), from the Upper Oligocene of Prambachkirchen, Austria; *Juglans* sp. (Beck, 1942a) from the Oligo-Miocene of Oregon; *Carya* sp. (Beck, 1942b) and *C. tertiara* (Prakash & Barghoorn, 1961), from Vantage, Washington; *Carya protojaponica* Watari (1952) and *Pterocarya rhoifolia* Sieb. & Zucc. (Watari, 1952), both from the Miocene of Japan; and *Pterocarya* sp. (Beck, 1942c) from the Miocene of Washington.

Juglans, with about 15 generally recognized species, is indigenous to China, Japan, India, Persia, the United States, Mexico, Central America,

the West Indies, and the Andean region of South America from Venezuela and Colombia to Argentina (Stark, 1953). Of the six species native to the United States, *Juglans cinerea* L. is widely distributed throughout most of the eastern half of the United States. *J. nigra* has much the same range as *J. cinerea* (Munns, 1938, maps 61, 62; Little, 1953).

The four western species are *Juglans microcarpa* Berlandier, *J. californica* S. Wats., *J. major* (Torr.) Heller and *J. hindsii* Jeps. None is native to the state of Washington (Little, 1953).

LEGUMINOSAE

4. **Leguminoxylon occidentale** Prakash & Barghoorn, sp. nov.

(FIGS. 24–27)

Growth rings: Distinct due to presence of terminal parenchyma; wood diffuse-porous (FIG. 27).

Vessels: Large to medium sized, 70–225 μ in tangential diameter, chiefly solitary (FIG. 27), often paired and rarely in radial or tangential rows of 3 cells, almost always encircled by sheaths of parenchyma cells, thick walled, the solitary vessels mostly elliptical, sometimes circular in cross section. Vessel elements about 200–450 μ long with usually truncate, sometimes tailed ends. Perforation plates exclusively simple. Intervascular pit-pairs (FIG. 25) bordered, alternate, oval to orbicular or angular where crowded, about 8–10 μ in diameter with lenticular apertures, often coalescent. Vessels almost always plugged with dark brown gummy substance.

Parenchyma: Paratracheal and terminal. Paratracheal parenchyma forming vasicentric sheaths 2 or 3 (4 or 5) cells thick round the vessels (FIGS. 24, 27), mostly becoming aliform with short wings, often confluent and connecting 2 or 3 pores tangentially or rarely forming radial extensions uniting vessels between the same pair of rays. Terminal parenchyma 1–3 (sometimes more) cells thick, forming a sharply defined line (FIG. 24) at the growth ring. Crystalliferous parenchyma rarely present.

Xylem rays: Homogeneous (Kribs Homogeneous Type 2), composed of procumbent cells, 1–5 cells wide (FIG. 26), unstoried; uniseriate and biseriate rays very rare, the uniseriate rays only few cells high; multiseriate rays mostly 3–5 cells broad and 0.75 mm. high; up to 6–10 rays per mm. Ray cells circular to oval in tangential section and 10–15 μ in diameter.

Imperforate tracheary elements: Libriform fibers polygonal in cross section, 8–15 μ in diameter, walls thick (FIG. 24) with a small lumen; nonseptate; pits apparently simple.

MATERIAL. A single small specimen of silicified, mature, secondary xylem.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55076.

The structural features of this fossil clearly indicate its affinity with the woods of Leguminosae and most closely with *Acacia*, *Cassia*, and other genera of similar wood structure. However, owing to the diversity, great

number of species, and range of structural variability within these genera, it does not seem possible to establish with any assurance its precise generic position. The nearest approach to the structure of the fossil which we have been able to establish is the genus *Acacia* and, within this genus, the species *A. ferruginea* DC. Our survey included the study of thin sections of the wood of nineteen species of *Acacia* and published descriptions of nine additional species (Kanehira, 1921b, pp. 89–90, *Pl. 18, fig. 106*; Pearson and Brown, 1932, pp. 439–445, 450–452, *figs. 150, 151, 154*; Kribs, 1959, pp. 60–62, *figs. 156, 158, 161, 394*). One aspect of the fossil which renders its identification more difficult is the tangential compression failure which preceded mineralization, thus exaggerating the ellipticity of the vessels as seen in transverse section. In view of these facts, it seems more desirable to designate the fossil to family, rather than to genus. Its affinity with the Leguminosae seems unquestionable. If the wood actually belongs to the genus *Acacia*, it is of some interest to note the present geographic distribution of the genus in relation to the fossil occurrence. The genus comprises some 450 species of trees and shrubs, of which 300 species are found in Australia alone, while the remaining species are widely dispersed through southeastern Asia, tropical and southern Africa, and tropical America, with extensions into temperate South America and the southern United States. Its nearest occurrence to the Vantage area is in southern California.

NYSSACEAE

5. **Nyssa eydei** Prakash & Barghoorn, sp. nov. (Figs. 1–5)

Growth rings: Fairly distinct, delineated by a narrow band of flattened, thick-walled fibers; wood diffuse-porous (Fig. 1).

Vessels: Small, 45–90 μ in tangential diameter (mean diameter 62 μ), solitary (Fig. 1) and in small radial multiples and groups, thin-walled, polygonal to oval (Figs. 1, 2) in cross section, quite uniform in size, numerous and fairly evenly distributed. Vessel elements up to 1700 μ long with tapering ends. Perforation plates exclusively scalariform with numerous thin bars (Fig. 5). Intervascular pit-pairs bordered, opposite, oval-rectangular, usually 5–10 μ in diameter with short linear apertures (Fig. 4). Vessels open.

Parenchyma: Not abundant, mostly diffuse, sometimes in short metatracheal rows (Fig. 2), occasionally paratracheal. Parenchyma cells mostly rectangular, sometimes crystalliferous.

Xylem rays: Heterogeneous, 1–3, rarely 4 cells wide (Fig. 3); uniseriate rays quite common, 2–29 (often 4–12) cells high; multiseriate rays mostly 3 cells broad and 1.75 mm. high; uniseriate rays and margins of multiseriate rays composed of few to many rows of mostly upright and square cells; vertical ray fusions common; up to 12–15 rays per mm. Ray cells thin-walled, round to vertically elongated in tangential section. 10–20 μ in diameter.

Imperforate tracheary elements: Fiber tracheids mostly rectangular to

polygonal in cross section (FIG. 2), large, 20–45 μ in diameter, walls thin with a fairly large lumen; nonseptate; pits bordered with slitlike apertures.

MATERIAL. A single specimen of silicified, mature, secondary xylem measuring 8 × 7 × 1.5 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 54972. The species is named for Mr. Richard H. Eyde, who is currently working on the fossil endocarps of *Nyssa*.

A survey of the structural features of the woods of *Nyssa* indicates that the nearest affinity of the fossil is with *Nyssa ogeche* Bartr. The structure of *Nyssa eydei* and that of *N. ogeche* are virtually identical in all major features. A few minor differences exist, however. The intervascular pit-apertures often tend to fuse in *Nyssa ogeche*, a feature not found in *N. eydei*; the metatracheal parenchyma is more frequent in *Nyssa eydei* than in *N. ogeche*, and the rays tend to have longer uniseriate wings which frequently fuse.

Despite the widespread occurrence of *Nyssa* and related genera represented as pollen and endocarp remains, the wood of *Nyssa* is very poorly represented in the fossil record. Its existence in the Russell Forests flora was noted by Beck (1945). The form genus *Nyssoxylon* Mädel includes the genera *Nyssa* and *Davidia*. *Nyssoxylon japonicum* Mädel (1959), from Japan, although somewhat resembling *Nyssa eydei*, differs in possessing tyloses in the vessels and in the narrower 1- or 2-seriate rays in contrast to rays 1–3 (rarely 4) seriate in *Nyssa eydei*.

In view of the rather limited distribution of *Nyssa* in both North America and Asia and since *Nyssa ogeche* is readily separable on the basis of wood structure from other species of the genus, the occurrence of a species closely resembling *N. ogeche* in the Tertiary of the northwestern United States is quite unexpected. *Nyssa ogeche* is a large swamp tree of currently limited distribution in swamps of the Coastal Plain of the southeastern United States, extending from South Carolina to northwestern Florida.

ULMACEAE

6. **Ulmus baileyana** Prakash & Barghoorn, sp. nov. (FIGS. 6–11)

Growth rings: Distinct; wood ring-porous. Transition between early and late wood abrupt (FIGS. 7, 8).

Vessels: Large vessels in the early wood, 160–256 μ in tangential diameter (mean 190 μ), solitary, arranged in three to four rows, rarely associated with small vessels (FIG. 7, 8), thin walled, the solitary vessels oval to elliptic in cross section. Vessel elements 130–460 μ long. Perforation plates exclusively simple, horizontal to sometimes slightly oblique. Intervascular pit-pairs (FIG. 6) bordered, alternate, orbicular or angular where crowded, 9–11 μ in diameter, with circular apertures; vessel-parenchyma pits numerous, more or less arranged in vertical rows, with fairly large oval apertures. Late-wood vessels small (FIG. 7), 50–160 μ in

tangential diameter (mean 81 μ), arranged in more or less continuous, wavy, tangential or oblique bands, usually polygonal due to clustering, occasionally round to oval in shape. Vessel elements with spiral thickenings. Perforation plates and intervascular pit-pairs similar to early-wood vessels, except smaller. Thin-walled tyloses common.

Parenchyma: Paratracheal and metatracheal-diffuse (FIGS. 8, 9). Paratracheal parenchyma occurring as few cells contiguous to the large vessels of early wood (but never forming a continuous sheath) and marginal to and occasionally included in the clusters of wavy bands of late-wood vessels and vascular tracheids. Diffuse parenchyma sparse, scattered among the fibers and occasionally in contact with the xylem rays. Parenchyma cells sometimes crystalliferous.

Xylem rays: Homogeneous (Kribs Homogeneous Type 2), composed of procumbent cells (FIGS. 10, 11), 1–6 cells wide; uniseriate rays rare, 2–10 cells high; multiseriate rays often fusiform, mostly 4 or 5 cells broad and 1.13 mm. high; up to 5–7 rays per mm. Ray cells slightly thick walled, circular to oval or vertically elongated in tangential section and 10–17 μ in diameter.

Imperforate tracheary elements: Libriform fibers and vascular tracheids. Libriform fibers polygonal in cross section, 10–22 μ in diameter, wall moderately to very thick (FIG. 9), with a small to fairly large lumen, nonseptate; interfiber pits simple. Vascular tracheids occasionally present both in the early-wood porous zone and in the clusters of late-wood vessels.

MATERIAL. A single specimen of silicified, mature, secondary xylem measuring approximately 12 $\times$ 6 $\times$ 6 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 54918. This species is named in honor of Irving W. Bailey, Professor of Plant Anatomy, *Emeritus*, Arnold Arboretum, Harvard University.

Structural features of this wood indicate its affinity with the genus *Ulmus*, two species of which have been described in our previous paper. Sufficient differences in structure exist, however, to justify its separation as a distinct species. The fossil wood closely resembles the wood of the modern species *U. rubra* Mühl. (*U. fulva* Michx.). It differs, however, from *U. rubra* in the presence of tyloses in the vessels, the larger late-wood vessels, the smaller amount of paratracheal parenchyma associated with the vessel clusters in the late wood, and the more crystalliferous wood parenchyma. In addition, the multiseriate rays are slightly broader and higher in *U. baileyana* than in *U. rubra*, and uniseriate rays are rare.

DISCUSSION

In our first paper (Prakash & Barghoorn, 1961) on the Vantage fossil woods, we indicated that the plants determined generically comprise an eastern American, a western American, and an Asiatic element. The present observations tend to confirm this geographic pattern. Of the genera

described, *Ulmus* and *Nyssa* occur in the eastern United States, whereas *Aesculus*, *Juglans*, and *Quercus* are found in both the eastern and western parts of the United States. The leguminous wood which is quite comparable to the genus *Acacia* indicates a more southern or Asiatic affinity.

Of the twelve woods of Vantage flora determined to genus, only two, viz., *Quercus* and *Acer*, have survived in the existing flora. The ecological conditions which may be inferred from the present distribution of many of the genera would indicate that the flora preserved in the Russell Forests existed under warm-temperate mesophytic conditions. This inference is further strengthened by closer comparison of the fossils with their living counterparts in terms of species, such as the close resemblance between *Nyssa eydei* and *N. ogeche*. The latter species is sharply delimited today by both temperature and edaphic conditions such as obtain in the humid swamp-forests of the southeastern United States. It is quite probable, in view of the ecological association of the Vantage genera, that the climate was featured by both higher annual average temperatures and by fairly high summer rainfall. The decimation of the mesophytic forests of the Miocene of central Washington was brought about by a combination of factors of which gradual refrigeration, culminating in Pleistocene glaciation was a major factor. In addition, re-entrance into this region in postglacial times of certain of these genera which possess cold tolerance has been prevented by the barrier of aridity induced by the Cascade uplift.

In addition to the kind help of those acknowledged in the preceding paper, the authors are also much indebted for that of Mr. Clarence Scammon, who aided the first author greatly in his field excursions in the Vantage area. The first author also wishes to acknowledge his sincere appreciation to the National Academy of Sciences, Washington, D. C., for the financial assistance given during this investigation.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–5. Wood of *Nyssa eydei*: 1, transverse section, × 37 — note vessel and parenchyma distribution; 2, transverse section magnified to show the cellular details, × 90 — note parenchyma distribution; 3, tangential section showing shape, size, and nature of xylem rays, × 90; 4, intervascular pitting, × 160; 5, scalariform perforation plate, × 110. FIGS. 6, 7. Wood of *Ulmus baileyana*: 6, intervascular pitting × 120; 7, transverse section, × 20 — note vessel distribution in late wood forming ulmiform bands.

PLATE II

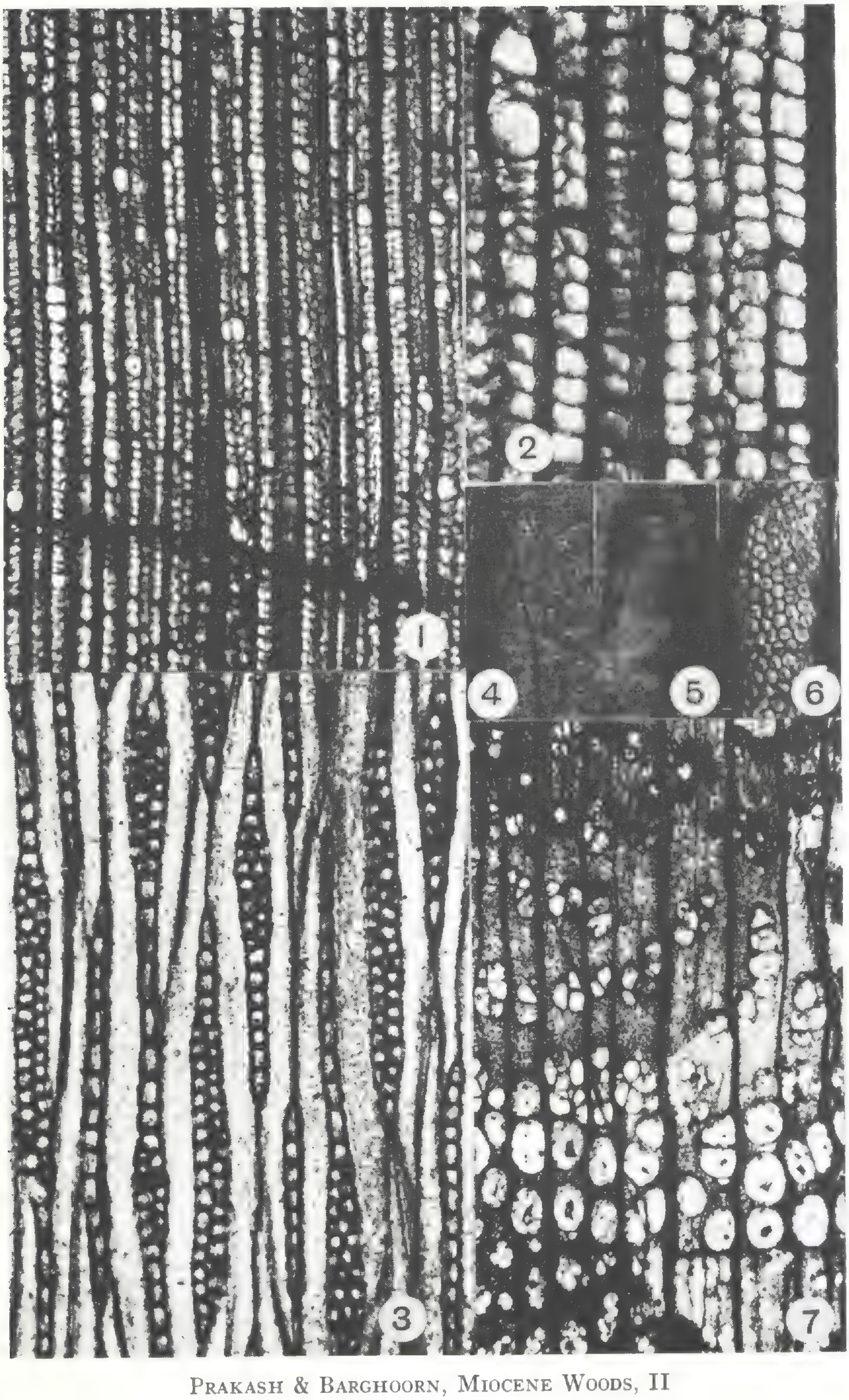
FIGS. 8–11. Wood of *Ulmus baileyana*: 8, transverse section slightly magnified to show early wood, × 30; 9, transverse section magnified to show fiber structure, × 90; 10, tangential section in low power showing shape, size, and distribution of xylem rays, × 30; 11, tangential section magnified to show ray structure, × 80. FIGS. 12–14. Wood of *Juglans fryxellii*: 12, intervascular pitting, × 160; 13, transverse section magnified to show structural details, × 60; 14, transverse section in low power, × 27 — note parenchyma distribution.

PLATE III

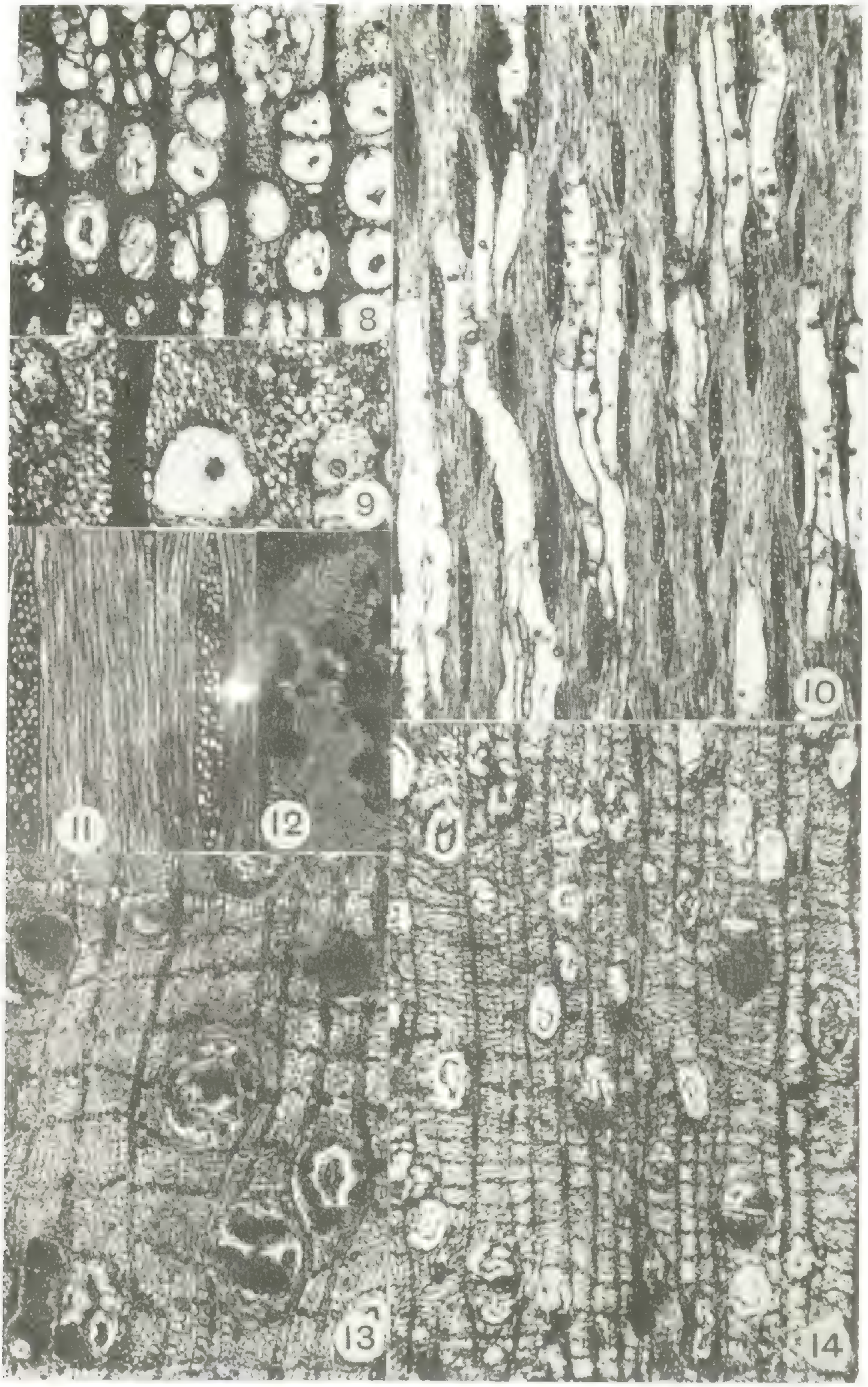
FIG. 15. Wood of *Juglans fryxellii*: 15, tangential section in low power, × 60 — note shape, size, and nature of xylem rays. FIGS. 16–19. Wood of *Quercus sahnii*: 16, tangential section, × 60 — note part of broad ray and numerous uniseriate rays; 17, transverse section magnified to show parenchyma and fiber structure, × 85 — also note thick-walled round vessels of late wood; 18, parenchyma with crystals, × 160; 19, transverse section in low power, × 27 — note large vessels in early wood and smaller vessels in late wood arranged in flame-shaped tracts. FIGS. 20–22. Wood of *Aesculus hankinsii*: 20, transverse section highly magnified to show the fiber cells, × 90; 21, intervascular pitting, × 240; 22, transverse section in low power to show vessel distribution, × 35.

PLATE IV

FIG. 23. Wood of *Aesculus hankinsii* in tangential section showing uniseriate xylem rays, × 90. FIGS. 24–27. *Leguminoxylon occidentale*: 24, transverse section magnified, × 60 — note parenchyma and fiber cells; 25, intervascular pitting, × 160; 26, tangential section, × 60; 27, transverse section in low power, × 26 — note vessel and parenchyma distribution.



PRAKASH & BARGHOORN, MIOCENE WOODS, II



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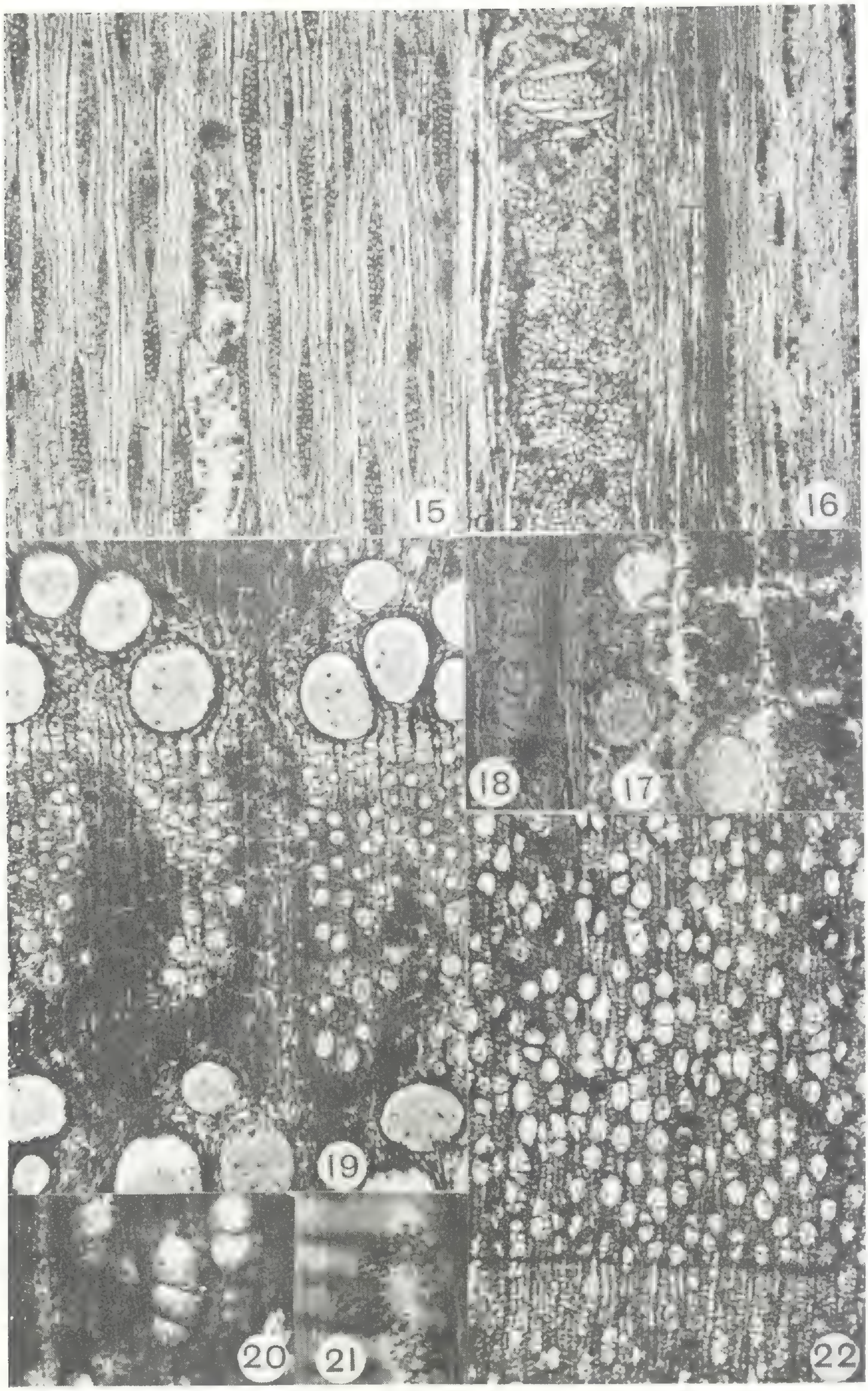

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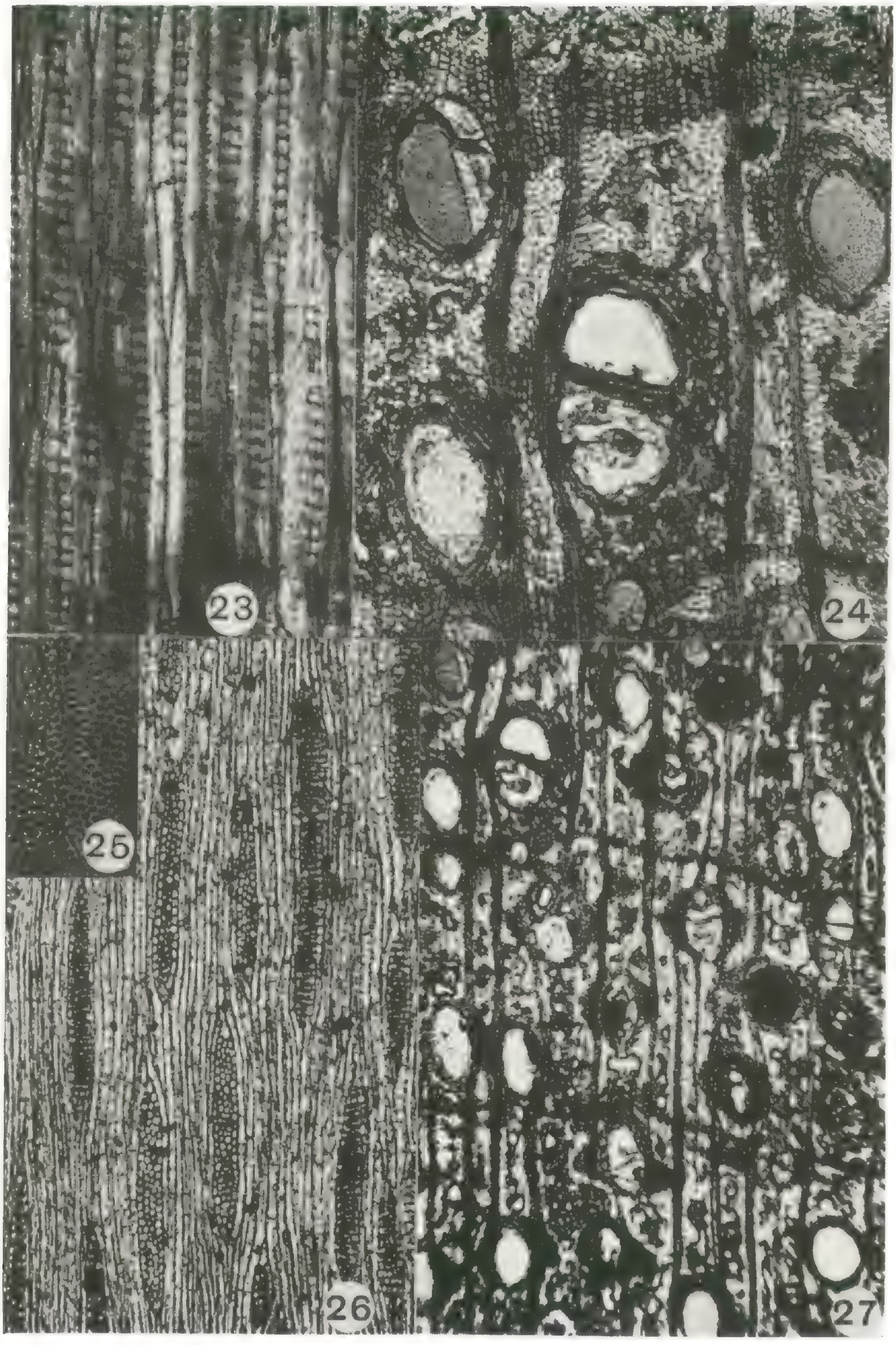

PRAKASH & BARGHOORN, MIOCENE WOODS, II

A SYNOPSIS OF THE GENUS COLUMELLIA (COLUMELLIACEAE)

GEORGE K. BRIZICKY

THE GENUS COLUMELLIA was founded by Ruiz and Pavón in 1794. Since 1801, when Ruiz referred the genus to Oleaceae (Jasmineae), the relationships of this Andean South American group of three or four woody species have been a perplexing problem for several generations of taxonomists. With its peculiar combination of opposite, exstipulate leaves; bisexual, epigynous flowers; somewhat irregular, sympetalous corollas; two stamens with plicate and contorted anthers resembling those of some Cucurbitaceae; two-carpellate, imperfectly two-locular ovaries; and imperfectly four-locular capsular fruits, *Columellia* is indeed a unique genus. It has been considered to be related to or has been placed in a whole series of families, including the Saxifragaceae, Lythraceae, Onagraceae, Ericaceae-Vaccinioideae, Ebenaceae, Styracaceae, Oleaceae, Gentianaceae, Scrophulariaceae, Gesneriaceae, Loganiaceae, Rubiaceae, and Caprifoliaceae. Although most recent taxonomists (following De Candolle, 1839) treat *Columellia* as a monogeneric family placed near Gesneriaceae, Wettstein (1935) stressed the uncertainty of its position. On the other hand, Solereder (1899), taking into consideration the anatomy of the genus, thought Collumelliaceae to be closely allied to Saxifragaceae, rather than to Gesneriaceae.

It is evident that gross morphology alone is inconclusive in solving this problem and that more attention must be paid to the anatomical, as well as embryological and cytological, characters of the taxa involved. In consideration of this, a comparative anatomical and taxonomic study has been undertaken by Dr. William L. Stern, Division of Woods, U. S. National Museum, Smithsonian Institution, and the author in the hope of shedding more light on the problem of the systematic position of Columelliaceae. The present study is then to be considered as a taxonomic introduction to this work, which is now in progress.

Columellia Ruiz et Pavón, Fl. Per. Chil. Prodr. 3. *pl. 1.* 1794, nom. cons. prop.[1]

Uluxia Jussieu, Dict. Nat. Sci. **10:** 103. 1818.

Ramose, evergreen shrubs or trees with shreddy bark; branchlets terete or obtusely quandrangular, usually more or less hairy, the internodes short. Leaves opposite, crowded, exstipulate simple, ± inequilateral, entire or toothed (teeth and leaf apices gland-tipped), pergamentaceous to

[1] *Columellia* Ruiz et Pavón, 1794, should be conserved against an earlier homonym, *Columella* Loureiro, Fl. Cochinch. 85. 1790 (nom. rejic. vs. *Cayratia* Jussieu, 1818, nom. cons.). See A. A. Bullock, Taxon **9:** 221. 1960.

coriaceous, with distinct or indistinct lateral nerves, the petiole usually short, margined (from the decurrent leaf blade), the opposite bases of petioles sheathlike, connate. Inflorescence axillary and/or terminal, basically a solitary dichasial cyme (sometimes reduced to a single central flower) or a small panicle of dichasia. Flowers bisexual, somewhat irregular, epigynous, short pediceled to subsessile, bibracteolate. Calyx tube narrowly to broadly obpyramidal or obconical, adnate to the ovary, the lobes 4–6 (8?), usually 5, subequal, each tipped with a gland, valvate or slightly imbricate in aestivation, accrescent. Corolla yellow, sympetalous, somewhat irregular, subrotate to subcampanulate, the tube short, the lobes 5 or 6 (8?), usually 5, slightly unequal, usually longer than the tube, imbricate in aestivation. Stamens 2, very rarely 3, attached at base of corolla tube, the filaments short and stout, adnate at base or for 1/3–1/2 of their length to the corolla tube, dilated at apex into a broad subcircular-reniform, sometimes inconspicuously 3–5-lobed, connective on which an extrorse, irregularly plicate and contorted anther is borne. Gynoecium syncarpous, 2-carpellate. Stigma broad, depressed-capitate, 2- or obscurely 4-lobed, ending a terminal, relatively short, stout style; ovary inferior, imperfectly 2-locular, with numerous anatropous, unitegmic and tenuinucellate ovules multiseriately attached to 2 much intruded parietal placentae. Fruit an imperfectly 4-locular, obpyramidal, obconical to subfusiform capsule, dehiscing septicidally into bifid valves; seeds numerous, minute, laterally compressed, ± oblong, smooth, the endosperm fleshy, the embryo minute, straight, axile.

LECTOTYPE SPECIES: *C. oblonga* Ruiz et Pavón; see Bullock, Kew Bull. 14: 41. 1960.

The genus includes three or four species occurring in the Andean region of Ecuador, Peru and western Bolivia at altitudes of from about 1600 to 3600 meters.

Morphological notes. In addition to the characteristics given in the formal generic description above, a number of other morphological details, some of which have been used in the delimitation of species, should be given.

The young branchlets, leaves (especially the lower surface), axes of the inflorescences, hypanthia, calyx lobes (at least the outer surface), and the exterior surface of the corolla tube usually are sericeous, appressed-puberulous, or more or less woolly. There is sometimes a tendency toward glabrescence, and rarely these parts are glabrous or subglabrous (*Columellia lucida*). The leaf apices and teeth, the bracts, and the calyx lobes usually are tipped with a mucro-like gland.

The data in the literature on the number of perianth parts show some discrepancies: calyx and corolla 5-merous (Ruiz & Pavón, 1794, 1798; Fritsch, 1894; Schlechter, 1920); or calyx 5-lobed, but corolla 5–8-lobed (De Candolle, 1839; Lindley, 1853; Bentham & Hooker, 1876); or calyx and corolla 5–8-merous (Engler & Diels, 1936). In this study only 5- and occasionally 6-lobed calyces and corollas and a single 4-lobed calyx have

been observed. The calyx lobes themselves are triangular-ovate to oblong, 0.25–0.5 cm. long, and 0.15–0.3 cm. broad, acutish or obtuse. The tube of the corolla varies from 0.15 to 0.55 cm. long, and the lobes are usually longer than the tube, more or less semicircular in outline, and 0.3–0.7 cm. long and 0.4–0.9 cm. broad. The diameter of the expanded corolla limb varies from 0.8 to 2 cm.

The stamens are usually two (the only number recorded for the genus), and these are alternate with the lateral and posterior (adaxial) corolla lobes. In a single flower of *Columellia oblonga* subsp. *oblonga* and in one of *C. obovata*, three stamens were present. The position of the extra stamen was different in both cases. In a single flower of *C. obovata* one subsessile and one sessile anther (anomaly?) were observed.

The stamens, with their peculiar plicate and contorted anther, have been regarded by some taxonomists as complex structures arising from the connation of two or three stamens. However, Van Tieghem (1903), on the basis of the anatomy of the stamens, affirmed their simple character and assumed a basic number of five stamens and the abortion of three.

The pollen, as described by Erdtman (1952), is "3-colporate, (oblate-) suboblate. Sexine thicker than nexine, rather finely reticulate (muri simplibaculate). Ora ± circular." The size of pollen grains varies from 25 × 34 μ in *Columellia oblonga* (Peru, *Weberbauer 7791*), to 24 × 31 μ in *C. obovata* (Peru, *Ruiz & Pavón*, 1788), to 22.5 × 29 μ in *C. sericea* (Peru, *Ruiz & Pavón*), according to Erdtman (1952).

Although some authors have mentioned the presence of a nectariferous disc (Lindley, 1853; Rusby, 1896), the author could not detect this in the dried herbarium material. The presence of a nectary on the top of the ovary is probable, however.

As mentioned in the generic description, the shape of the capsules in *Columellia* varies from obpyramidal or obconical to subfusiform. The subfusiform shape is due to the growth of the top of the ovary after anthesis. In *Columellia oblonga* subsp. *sericea*, the length of the inferior portion of the fusiform capsule (that united with the calyx tube) varies from 0.3–0.6 cm., and the length of the superior free part of the fruit varies from 0.15–0.7 cm. Since fruits, in general, are very scantily represented in the herbarium material, possible specific differences in the shape and size of fruits and seeds could not be studied.

The general anatomy of *Columellia*, which seems to be fairly uniform within the genus, was studied by Solereder (1899) and Van Tieghem (1903). The wood anatomy of *C. oblonga* subsp. *sericea* was reported on by Record and Hess (1943).

Uses. The very bitter leaves of *Columellia oblonga* subsp. *oblonga* and *C. obovata* are used by natives in Peru as an infusion or decoction, sometimes as a powder, against tertian fever, and also serve as a stomachic (Ruiz & Pavón, 1798). The very hard wood of *C. oblonga* is (or was) utilized for manufacturing handles and various utensils in Peru (Ruiz & Pavón, *loc. cit.*) but only for fuel in Ecuador (Record & Hess, 1943).

KEY TO THE SPECIES

A. Leaves pergamentaceous to subcoriaceous, with 5–10 pairs of distinct, ascending lateral nerves, mostly 3–6 cm. long, conspicuously inequilateral, sericeous or appressed-puberulous on the lower surface; flowers usually in small panicles; corolla subrotate to subcampanulate; shrubs or trees. ..... 1. *C. oblonga.*

A. Leaves coriaceous, with indistinct lateral nerves, mostly 1–3 cm. long, inconspicuously inequilateral, glabrous or ± woolly pubescent on the lower surface; flowers in 1–3-flowered cymes; corolla subrotate; shrubs, sometimes low.

B. Leaves glabrous on the lower surface, oblanceolate and or ovate-cuneate, entire or rarely 1- or 2-dentate at apex, 1–3 cm. long. ..... 2. *C. lucida.*

B. Leaves pubescent on the lower surface, elliptic-oblong to broad-obovate.

C. Leaves all entire, subsericeous on the lower surface, elliptic-oblong to elliptic-obovate, 0.9–1.3 cm. long; flowers ca. 0.8 cm. in diameter; low shrubs. ..... 3. *C. subsessilis.*

C. Some or most leaves remotely dentate, densely or sparsely sublanuginous or subtomentulose on the lower surface, oval, elliptic- to broad-obovate, 1–2.7 cm. long; flowers 0.9–2 cm. in diameter. ..... 4. *C. obovata.*

1. **Columellia oblonga** Ruiz et Pavón, Fl. Per. Chil. 1: 28. *pl. 8, figs. a & 1–8.* 1798.

C. arborescens Pers. Syn. Fl. 1: 13. 1805.

DISTRIBUTION: Peru, Ecuador, and western Bolivia.

KEY TO THE SUBSPECIES

A. Leaves glandular-serrulate to -serrate, at least toward apex, appressed-puberulous on the lower surface; corolla subrotate, the tube (0.15)0.2–0.3 cm. long, as long as or shorter than calyx lobes; staminal filaments adnate to corolla tube only at base.

B. Leaves glandular-serrulate toward the apex (rarely entire), oblong, elliptic or oblanceolate-oblong, 3–4.5 cm. long, obtuse, rarely acute; corolla tube appressed-puberulous externally. ..... 1a. subsp. *oblonga.*

B. Leaves glandular-serrate from near middle to apex, elliptic to elliptic-oblong, 4–6 cm. long, acute or obtuse; corolla tube nearly glabrous externally. ..... 1b. subsp. *serrata.*

A. Leaves entire, rarely with a few teeth near apex, usually densely sericeous on the lower surface (very rarely appressed-puberulous), oblanceolate to elliptic-obovate, (1.6)3–5.2 cm. long and 0.5–2.3 cm. broad, usually acute; corolla usually subcampanulate, the tube (0.3)0.4–0.55 cm. long, appressed-pilose externally, mostly longer than the calyx lobes; staminal filaments adnate to corolla tube for 1/3–1/2 of their length. ..... 1c. subsp. *sericea.*

1a. **Columellia oblonga** subsp. **oblonga** (TYPE: Pillao, *Ruiz & Pavón*).

Peru. AMAZONAS: Chachapoyas, *Mathews 1319* (NY). HUÁNUCO: Pillao, *Ruiz & Pavón* (F, isotype) Pillao on the side of river Chaglía-monte, alt. 2700

m., *Woytkowski 34067* (F, MO). AYACUCHO: La-Mar, between Tambo and Apurimac, way of Osno, alt. 2900–3000 m., *Weberbauer 5584* (F, GH, US). CUZCO: Urubamba, Machu Picchu, alt. ca. 2100 m., *Cook & Gilbert 850* (US), alt. 2000 m., *Vargas 7408* (US), Machu Picchu y Huayana Picchu, 2400 m., *Scolnik 830* (NY); Quispicanchi, Marcapata, *Weberbauer 7791* (A, F, MO, US); San Miguel, Urubamba Valley, alt. ca. 1800 m., *Cook & Gilbert 1749* (US). **Ecuador.** AZUAY: Eastern Cordillera, 1 8 km. north of the village of Sevilla de Oro, alt. 2400–2700 m., *Camp E–4461* (GH, NY, Y).

This subspecies has usually been described as a shrub or small tree up to 6 m. high. Camp, however, collected his herbarium specimen from a tree 20 m. tall. In a field note with this specimen he says, "This species flowers when quite young, specimens seen in the region in full flower and only 1 meter high; it is fairly abundant on cut-over and burned areas which are regenerating (probably from root-sprouts) where it might be taken for a shrub; also seen in forested areas, the tree easily detected by the irregular contour of the trunk and shreddy bark, one patriarch seen along this same quebrada at about 8000 ft. elev. with a trunk diam. of nearly 2 meters (the top broken out of this tree and so no estimate can be given of the maximum height)." Camp's collection, the first of subsp. *oblonga* from Ecuador, is also interesting as it represents a form of the subspecies with predominantly entire leaves intermixed with two-to-few-dentate leaves. In this character the form approaches subsp. *sericea*. There are no grounds, however, for a supposition of hybridization (at least recently), for no specimens of the latter subspecies have been seen or recorded from Prov. Azuay. Furthermore, our knowledge of variations of subsp. *oblonga* (even on individual trees) is very limited. Camp's field note suggests a further source of variation, regeneration from the root sprouts, which could result (at least on younger plants) in larger, perhaps more dentate and more densely pubescent leaves and larger flowers than in plants grown from seeds or in adult specimens. In addition, *Mathews 1319* seems to be intermediate between this subspecies and subsp. *sericea*.

In Ruiz's *Travels* (1940) this subspecies is mentioned as *Columellia corymbosa*.

1b. **Columellia oblonga** subsp. **serrata** (Rusby) Brizicky, stat. nov.

C. serrata Rusby, Mem. Torrey Bot. Club **6:** 93. 1896. (TYPE: *Miguel Bang 1172*).

Bolivia. COCHABAMBA: Espirito Santo, *Miguel Bang 1172* (NY-holotype; A, F, MO, US-isotypes).

The type locality, Espirito Santo, is in the "yungas" floristic region at an altitude of ca. 1600 m. (Herzog, 1923). Unfortunately, the specimen *Herzog 2240*, ("Baumstrauch im Gebüsch über Incacorral, ca. 2700–2800 m.") reported by Herzog (1915) as *Columellia serrata* has not been seen. Schlechter (1920) says regarding the specific differences between *C. serrata* and *C. oblonga*, "Bei näherem Vergleich der Art mit *C. oblonga* Ruiz & Pav. zeigt sich, dass beide recht nahe verwandt sind. Ich halte sie hier

getrennt, weil bei *C. serrata* Rusby die Blätter meist deutlich grösser und die Blüten fast kahl sind, während die letzteren bei *C. oblonga* Ruiz & Pav. aussen nach dem Grunde zu ziemlich dicht, wenn auch sehr kurz behaart sind. Ausserdem scheinen bei *C. serrata* Rusby die Früchte mehr denen der *C. sericea* H. B. & Kth. zu ähneln." These differences by themselves can hardly be considered of specific significance. Furthermore, the density of pubescence of the corolla tube in *C. oblonga* subsp. *oblonga* varies to a considerable degree; for instance, the corolla tube in *Weberbauer 5584* is almost glabrous outside, as is that of *C. serrata*. The latter is therefore reduced to subspecific rank under *C. oblonga*.

1c. **Columellia oblonga** subsp. **sericea** (HBK.) Brizicky, stat. nov.

C. sericea HBK. Nov. Gen. Sp. **2:** 388. 1818 (TYPE: *Humboldt & Bonpland 3204*).

C. Mathewsii Briquet, Ann. Conserv. Jard. Bot. Genève **20:** 367. 1919 (TYPE: Chachapoyas, *Mathews*).

VERNACULAR NAMES: quinoa blanca (Rimbach), pantza (Acosta Solís).

Ecuador. IMBABURA: Lake Cuicocha, alt. 3200 m., *Penland & Summers 738* (COCO, F), Lake Cuicocha, Islote Chica, alt. 3150 m., *Aspland 7152* (US); small wooded quebrada 5 km. north of Hacienda Pinnon, *Wiggins 10351* (DS). PICHINCHA: M. Pichincha, *Ed. André K-588* (F); Malchingui to Pomasqui, alt. 3000–3600 m., *A. S. Hitchcock 20846* (GH, NY, US); Valle Seco del Pedregal, Cord. Oriental, *Acosta Solís 8433* (F); Pifo, *Mille 409* (US); Pululahua, *Ed. André 3798* (F, GH); Calacali, Western Andes of Quito, 3000–3300 m., *Lehmann 4055* (F, US); Bajada de Lache a Condor Machay, Cord. Occ., alt. 2700–3100 m., *Acosta Solís 7004* (F); San Juan, Cord. Occidental, Camino a Saloya, alt. 3200 m., *Acosta Solís 10500* (F). TUNGURAGUA: Tunguragua, *Humboldt & Bonpland 3204* (F-photograph of type; F, US-isotypes); vicinity of Patate, hacienda Leito, alt. ca. 2900 m., *Asplund 8003* (US). BOLIVAR: Pajonal de Gualicon Loma, Cord. Occ. alt. 3240 m., *Acosta Solís 6264* (F). CHIMBORAZO: Ad pagum Penipe, in reg. arborea superiori, alt. 2500–3200 m., *Mille 44* (A, GH, NY, US). GUAYAS: Guayaquil, in 1804, "*Ruiz & Pavón*" (F [2]). Loco speciali haud indicato: Andes of S. America, *U. S. Dep. Agr.* (US); in Andibus Ecuadorensibus, *Spruce 5468* (GH); *Jameson* (US 534966, US 534793, US 534794); inner slope of Eastern Cordillera, alt. 3400 m., in bush, *Rimbach 30* (F, GH, Y), 3200 m., *Rimbach 81* (A), *Rimbach 122* (A, F, Y), *Rimbach 227* [3] (US). **Peru.** AMAZONAS: Chachapoyas, *Mathews s.n.* (G-holotype of C. *Mathewsii*).

Subspecies *sericea* seems to be very distinctive, not only in its usually entire, very rarely toothed leaves, which are sericeous on the lower surface

[2] The label on this specimen bears the heading: "Ex antiquo herbario generali Herbarium Horti Botanici Matritensis Plantae a 'Ruiz et Pavón' in vice-regno Peruviano et Chilensi lectae (1778–1788)." On the label is typed: "Guayaquil in 1804." This specimen was apparently collected by Juan Tafalla, a disciple of Ruiz and Pavón, who at about that time collected cinchonas for Ruiz in the mountains of Guayaquil, Loja, and Quito, Ecuador. (See Ruiz, 1801.)

[3] Most probably *Rimbach 81* and *Rimbach 227*, cited here, are misnumbered and are, in fact, *Rimbach 122*, since in Rimbach's original list of field numbers in the Record Memorial Collection, Yale University, *Rimbach 81* is *Nicotiana Pavonii* Dunal, and *Rimbach 227* represents *Siparuna echinata* (HBK.) A. DC.

(e.g., *Hitchcock 20846*, and specimens cultivated in the 1870's at Kew, according to Schlechter, 1920), but also in its usually subcampanulate corollas, the tube of which usually is longer than the calyx lobes. Two exceptions, however, are *Mathews s.n.* (type of *C. Mathewsii*) and *Asplund 8003*, which have subrotate corollas with tubes shorter than the calyx lobes. (The former specimen also has leaves appressed short-pilose on the lower surface.) The diameter of the expanded corolla limb varies from one to two centimeters. The occurrence of such individuals transitional in these respects between *Columellia oblonga* and *C. sericea* is ample reason to regard both as components of a single species.

2. **Columellia lucida** Danguy et Chermezon, Bull. Mus. Hist. Nat. Paris. **28**: 436. 1922 (TYPE: *Rivet 740*).

C. Andrei Macbride, Publ. Field Mus. Bot. **4**: 92. 1925 (TYPE: *Ed. André K–1444*).

Ecuador. LOJA: Chuquiribamba, *André K–1444* (F-holotype of *C. Andrei*; GH-isotype). Cerro de St. Barbara,[4] *André 4500* (F, GH, NY-paratypes of *C. Andrei*).

The type of *Columellia lucida* was collected in Cerro Narihuiña ("Nairihuiña"), alt. 3900 m., in the Cordillera Chanchan, Prov. Azuay, Ecuador. Although the type has not been examined, the author has no doubts of the conspecificity of *C. lucida* and *C. Andrei*. The descriptions of the two are almost identical. The only differences noted are ovate-cuneate leaves, 1–1.5 cm. long, sometimes one- or two-dentate at the apex, in *C. lucida*, as against oblanceolate leaves, 1.5–3 cm. long and completely entire, in *C. Andrei*. If one takes into consideration that many smaller (younger) leaves in *C. Andrei* may be described as ovate-cuneate and that the presence of one or two teeth can hardly be an essential character, especially in this genus, the differences between these taxa appear to be insufficient for the recognition of two separate species. Their occurrence in adjacent provinces of Ecuador should also be noted. Leaves of this species (as represented by *C. Andrei*) strikingly resemble those of some specimens of *C. oblonga* subsp. *sericea* (e.g., *Acosta Solís 8433*, *Asplund 7152*, *Penland & Summers 738*), but are smaller than in the latter (as are the flowers) and are glabrous on the lower surface. When more material is available *C. lucida* may eventually prove to be treated best as a variety of *C. oblonga* subsp. *sericea*.

3. **Columellia subsessilis** Schlechter, Notizbl. Bot. Gart. Berlin 7: 356. 1920 (TYPE: *A. Stubel 45a*).

Bolivia. Yungas, mas ariba de Taca, 3300 m., Dec. 10, 1876, *A. Stubel 45a* (F-photograph).

[4] The exact geographic position of this locality has not been determined. It is possible, however, that Cerro St. Barbara is in Prov. Loja, since *André 4446* (*Passiflora sanguinolenta* Mast.) was collected near Chuquiribamba.

This species is known only from the type collection. According to Schlechter (1920), *Columellia subsessilis* differs from *C. obovata* in the habit, being a low dense shrub; in the relatively narrow, apparently always entire leaves subsericeous on the lower surface; in the subsessile inflorescences and flowers; in the smaller corollas; and in the remarkably short filaments of the stamens. These differences do not seem to be sharp ones and are hardly of specific significance, with the possible exception of the small flowers and very short filaments of the stamens. However, the constancy of the two latter characters as well as that of the entire leaves, in *C. subsessilis* has to be proved on more abundant herbarium material of this species. The available flowers of the taxa concerned are very few, but it may be noted that one subsessile anther (with a very short filament) and one completely sessile anther were observed in a flower of *C. obovata*, suggesting that this may not be a constant feature.

At present, *Columellia subsessilis* appears to be a variant of *C. obovata*, but for lack of conclusive data it is here maintained at specific rank.

4. **Columellia obovata** Ruiz et Pavón, Fl. Per. Chil. 1: 28. *pl. 12, figs. b & 1–7*. 1798 (TYPE: Tarma, *Ruiz & Pavón*).

C. frutescens Pers. Syn. Pl. 1: 13. 1805.
C. Weberbaueri Schlechter, Notizbl. Bot. Gart. Mus. Berlin 7: 358. 1920 (TYPE: *Weberbauer 3241*).

VERNACULAR NAMES: ulux, ullus, usluss (*Columellia obovata*); zocetullu, tsoquetullu (*C. Weberbaueri*).

Peru. JUNIN: Tarma, *Ruiz & Pavón* (F-photograph of type; isotype). ANCASH: Prov. Huaylas, encima de Caráz, Cordillera Blanca, alt. 3200–3400 m., *Weberbauer 3241* (F-photograph and small fragment of type of *C. Weberbaueri*; G-isotype; USM-small fragment of isotype); Prov. Huarás, circa á La Portada (Pacharuri), Cordillera Blanca alt. 3500 m., *Velardo Nuñez 3309* (US). AYACUCHO: Prov. Huamanga, between Totorabamba and Ayacucho, alt. 3300–3400 m., *Weberbauer 5482* (F, GH, US). CUZCO: Valle del Urubamba, Ollantaitambo, alt. 2800 m., *Herrera 3451* (F). URUBAMBA: Pumahuanca, alt. 3100–3500 m., *Vargas 7693* (MO, US). Without indication of locality, but probably in the vicinity of Tarma: *Dombey* (F, US).

According to Schlechter (1920), *Columellia Weberbaueri* differs from *C. obovata i*n the more vigorous growth; larger, dull leaves; more villous pubescence; larger flowers, ca. 2 cm. in diameter; and narrower calyx tube. None of these characters seems to be of specific significance. The dullness of leaves in *C. Weberbaueri*, as a characteristic of the living plant (rather than of a dried herbarium specimen) should be questioned. *Weberbauer 3241*, identified by Schlechter as *C. obovata*, has mostly dull (but some lustrous) leaves, but in all other respects it looks very much like a "small-leaved" *C. Weberbaueri*. The difference between "sublanuginous" pubescence in *C. Weberbaueri* and "subtomentulose" in *C. obovata* is not a sharp one, and both kinds are certainly only small variations of the same

basic type. Although the type specimen of *C. Weberbaueri* possesses somewhat larger flowers than *C. obovata,* another specimen from the same geographic and floristic province (Cordillera Blanca) which agrees with *C. Weberbaueri* in its vegetative organs, has flowers about 1 cm. in diameter. Thus, with these indications of intergradation, *C. Weberbaueri* is reduced here to the synonymy of *C. obovata*. .

The presence of at least a few dentate leaves has been given as a diagnostic character of *Columellia obovata*, but the species certainly is very variable, especially in dentation and pubescence of leaves. Although the type specimen of *C. obovata* shows a few leaves with dentate margins, there are other herbarium specimens in which it is hard to find a single leaf with even one or two teeth. On the other hand, specimens in which most of the leaves are markedly toothed have been seen. Thus the species either includes populations with entire, intermediate, and toothed leaves, or the dentation of leaves is an inconstant character reflecting the local ecological conditions. It seems likely that variation in size of the flowers is connected, not only with local ecological conditions, but also with the season. Perhaps in the future the necessity of subdividing *C. obovata* into two or more morphological-ecological types will be clear, but on the basis of the present data the recognition of any intraspecific categories within this species would be groundless.

This species is referred to as *Columellia ovalis* in the translation of Ruiz's *Travels* (1940).

CONCLUSIONS

The genus *Columellia* does not appear to be polytypic. Variations, although not uncommon, are usually limited to the vegetative organs, especially the leaves (size, degree of dentation, and pubescence). When variations involve the flower, as in *C. oblonga* subsp. *sericea* (subcampanulate corollas, stamens adnate to the corolla tube for 1/3–1/2 their length), they do not seem to be entirely fixed. Only four of the nine species which have been described are recognized in the present paper, and it is likely that still further reductions will be necessary as more adequate material is obtained. Field studies accompanied by extensive collecting, experimental cultures, and cytogenetic investigations are desirable to check the outlines of the taxonomy of the genus as proposed in this study, which has, of necessity, been based entirely upon scanty herbarium material.

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Connecticut; to Dr. R. A. Howard, director of the Arnold Arboretum; and to Dr. C. E. Kobuski, curator of the Arnold Arboretum and Gray herbaria, for arranging loans of specimens from herbaria in this country and abroad.

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A REVISION OF THE ASIATIC GENUS ENKLEIA (THYMELAEACEAE)

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THIS STUDY OF ENKLEIA is the second of three revisions treating the three genera which comprise the subtribe Linostomatinae of the Thymelaeaceae. It completes the revision of the two Asiatic members, *Linostoma* Wall. ex Endl. and *Enkleia* Griff., and prepares the way for a more enlightened appraisal of the Amazonian genus *Lophostoma* Meissn.

The members of the Linostomatinae have been combined taxonomically in various ways in the past so that a taxonomic re-evaluation is of primary importance. The revision of *Linostoma* and *Enkleia* has resulted in the reduction of the number of species and the alignment of several taxa with *Enkleia*, rather than with *Linostoma*. There is little doubt that *Lophostoma* is related to both *Linostoma* and *Enkleia*, as is evidenced by the common possession of a number of diagnostically important morphological and anatomical characteristics. An effort has been made to include, as a secondary study, certain anatomical information which may prove to be taxonomically significant. The large geographic disjunction that now exists between the South American and the Asian genera adds to the fascination of the interrelationships to be found among members of the subtribe.

SPECIAL MORPHOLOGY

Some of the more interesting morphological features found within the genus *Enkleia* are presented in this section. In addition, a deliberate and conscientious attempt has been made to parallel closely the discussion of morphological characteristics of *Linostoma* (Nevling, 1961). This has been done to simplify comparisons between the two genera. Additional morphological information can be found in the description and in the discussion following each species.

Gross and microscopic structure of the leaf was studied by clearing and staining with safranin or with ferric chloride and tannic acid. In addition, it was studied from safranin-fast green-stained cross and longitudinal thin sections, as was the petiole. This material was tested with phloroglucin and

hydrochloric acid, as well as with potassium iodide and sulphuric acid, to estimate chemically the degree of lignification of certain tissues.

The stem and inflorescence axes were studied by means of free-hand sections which were stained with either safranin or phloroglucin and hydrochloric acid. This technique was also employed with inflorescences and young shoots.

Flower structure was studied from material that was cleared and stained with safranin. In this instance, the study was limited to whole mounts and did not include sectioned specimens. The source material was from herbarium specimens in all instances, and the details of the techniques outlined above can be found in a previous paper (Nevling, 1961).

Vegetative Morphology. The vegetative axis is monopodial. Leaf position is opposite or subopposite except in extremely vigorous young shoots. In slow-growing shoots a cycle composed of an elongate internode and an extremely shortened internode accounts for the opposite to subopposite position, the trace for one leaf departing from the stele prior to the initiation of the second trace. In vigorous shoots, all internodes undergo similar elongation, thus accounting for the alternate leaf position. A single trace per node is formed in all cases, and the resultant gap is unilacunar.

Unequal bifurcations and trifurcations of the shoot are not unusual in *Enkleia* but do not occur with the frequency found in *Linostoma*. They are induced more generally by damage to the terminal bud which allows the development of subtending axillary buds in a haphazard manner, but, in some cases, the trichotomies occur without apical damage (see *Put 2305* and the flowering sheet of *Van Royen 3592*). In the Van Royen collection the opposite axillary branches are gracefully curved (not recurved) and the subtending leaves are borne a considerable distance above the point of external branching. The lowest leaf on these branches is unpaired and is the displaced leaf of the subtending node; the trace for this leaf has its origin below the point of external branching. It seems that the leaf is borne upon the axillary branch which it subtends. In reference to the "misplaced" leaf one should not expect to find a bud in its axil, but an axillary bud is almost invariably present. It is impossible to account for this unless it is a supernumerary bud.

In several specimens of *Enkleia malaccensis* (*Toroes 4099* and *Ridley 6427*) development of multiple axillary buds has occurred. In the Toroes specimen two axillary branches develop from the axil of a single leaf and are positioned one above the other. A specimen of *E. siamensis* ssp. *siamensis* (*Kerr 16136*) has the terminal bud injured, and supernumerary axillary buds have developed (three from one leaf axil, two from another). In the subgenus *Neivira* of the genus *Daphnopsis* supernumerary axillary buds are the rule, rather than the exception, and allow the plants to become cauliflorous. After examining the beautiful photograph of a *Phaleria* in Hou's treatment of the Thymelaeaceae (1960), I suspect that the same phenomenon is acting in that genus.

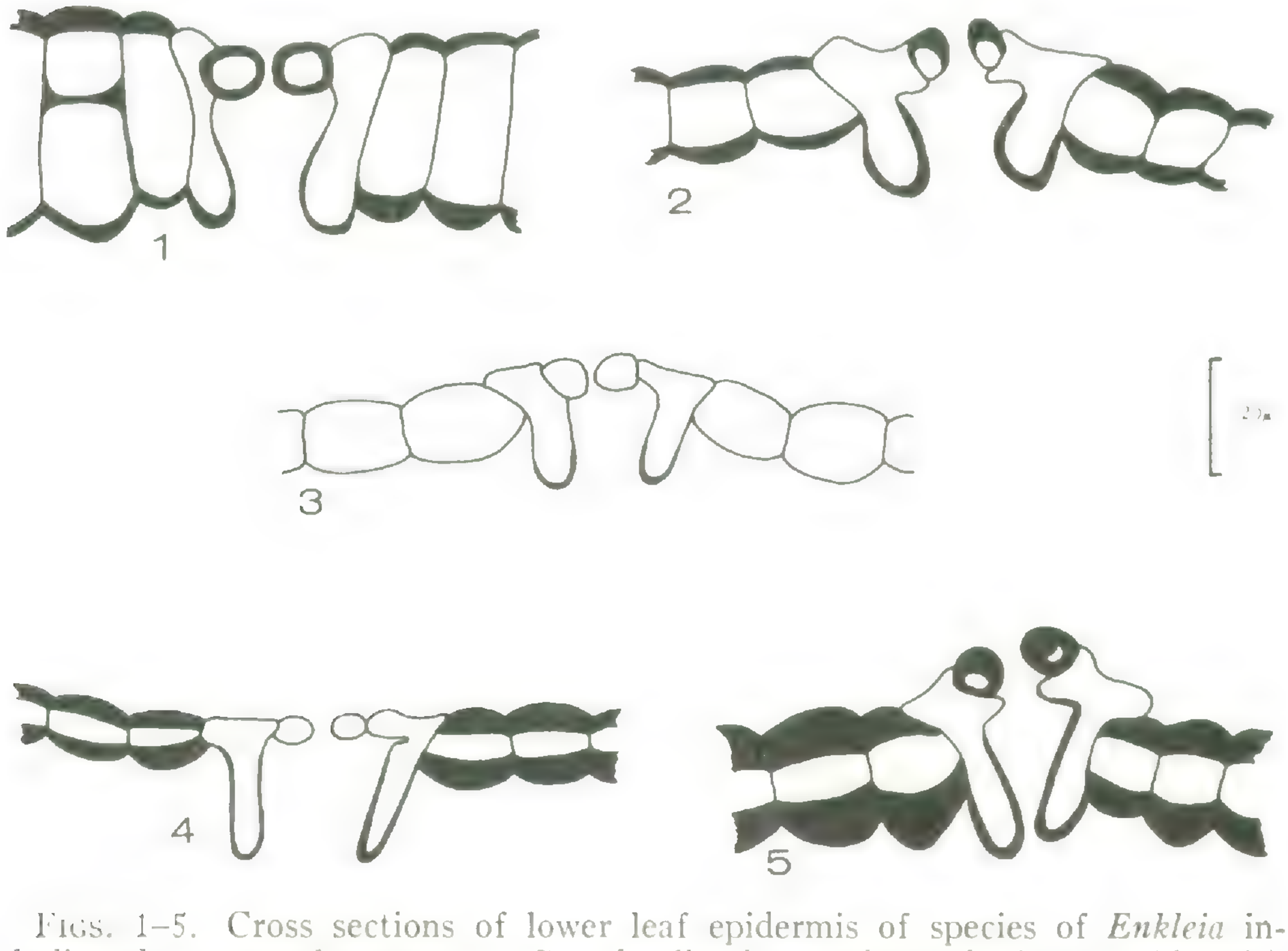
Axillary branches sometimes become gently to strongly uncinate, facilitating climbing. Such branches are quite thickened towards the base and bear very reduced leaves. The frequency of these modified branches varies rather widely, but some generalizations about their occurrence among the species may be made. *Enkleia thorelii* lacks them altogether; in *E. paniculata* and *E. siamensis* they are found infrequently but may be well developed; and in *E. malaccensis* they are found generally, sometimes very well developed (*Anta 1713*, for example).

The extraxylary fiber sheath surrounding the stele, by which the family is often identified, is well developed in this genus. It becomes well lignified after a number of years. In addition, in the pith are found scattered fibers which also appear to be well lignified. In general, the fibers and xylem of the *Enkleia* species are lignified to a greater extent than the corresponding structures in *Linostoma*.

The leaves are dorsiventral. The upper epidermis is composed of tabular cells, is unbroken by stomata, and is very poorly cutinized. In *Enkleia siamensis* and *E. paniculata* the upper epidermis is a single cell thick, with the periclinal walls much thicker than the anticlinal walls. There is a possibility that these differentially thickened cells may be slime cells. A single epidermal layer is found also in *E. malaccensis*, but the cell walls are not differentially thickened. *Enkleia thorelii* is unusual because the epidermis is one or two cells thick, varying irregularly with neither number predominant. When double, the two cells occupy the same volume as that occupied by the single cell components. The palisade tissue is composed of compact columnar cells and is two or three cells thick, except in *E. paniculata* in which it is only one or two cells thick. In all species, the palisade cells are smaller in diameter than the cells of the upper epidermis. A spongy parenchyma layer underlies the palisade and is composed of loosely knit branched cells interspersed with many large air spaces. This layer is developed to the fullest in *E. paniculata* in which it occupies fully three-quarters of the entire depth of the leaf. The lower epidermis is composed of cells smaller than those of the upper epidermis, and, in addition, it is interrupted frequently by stomata. In *E. siamensis*, *E. paniculata* and *E. malaccensis* it is uniseriate, the individual cells with the outer periclinal wall slightly bullate. The periclinal cell walls are differentially thickened in *E. siamensis* and *E. paniculata* but not in *E. malaccensis*. As might be expected, the lower epidermis in *E. thorelii* occasionally is double, and the individual cells are short-columnar with conspicuously bullate outer periclinal walls.

The stomata of all species of this genus are of the pit-type previously described for *Linostoma decandrum* (Roxb.) Wall. ex Endl. These stomata, when examined microscopically in cleared material stained with ferric chloride, resemble in face view many small doughnuts scattered on the lower leaf surface. A slight shift in focus is necessary to observe the guard cells. As in *L. decandrum*, a rosette of accessory cells surrounds each stoma, the number being rather variable (generally eight, nine, or ten, but as few as six and as many as thirteen). Each accessory cell is

somewhat awl-shaped and extends beyond and slightly over the guard cells, forming an urceolate or campanulate structure. Occasionally an accessory cell can be found being shared by two adjoining stomata. The guard cells are borne at the base of the accessory cells and are situated at most only slightly above the lower epidermis. Differences in the structure of the stomata can be found among the species (FIGS. 1–5), but the amount of variation has not been determined, so their taxonomic worth cannot be evaluated.

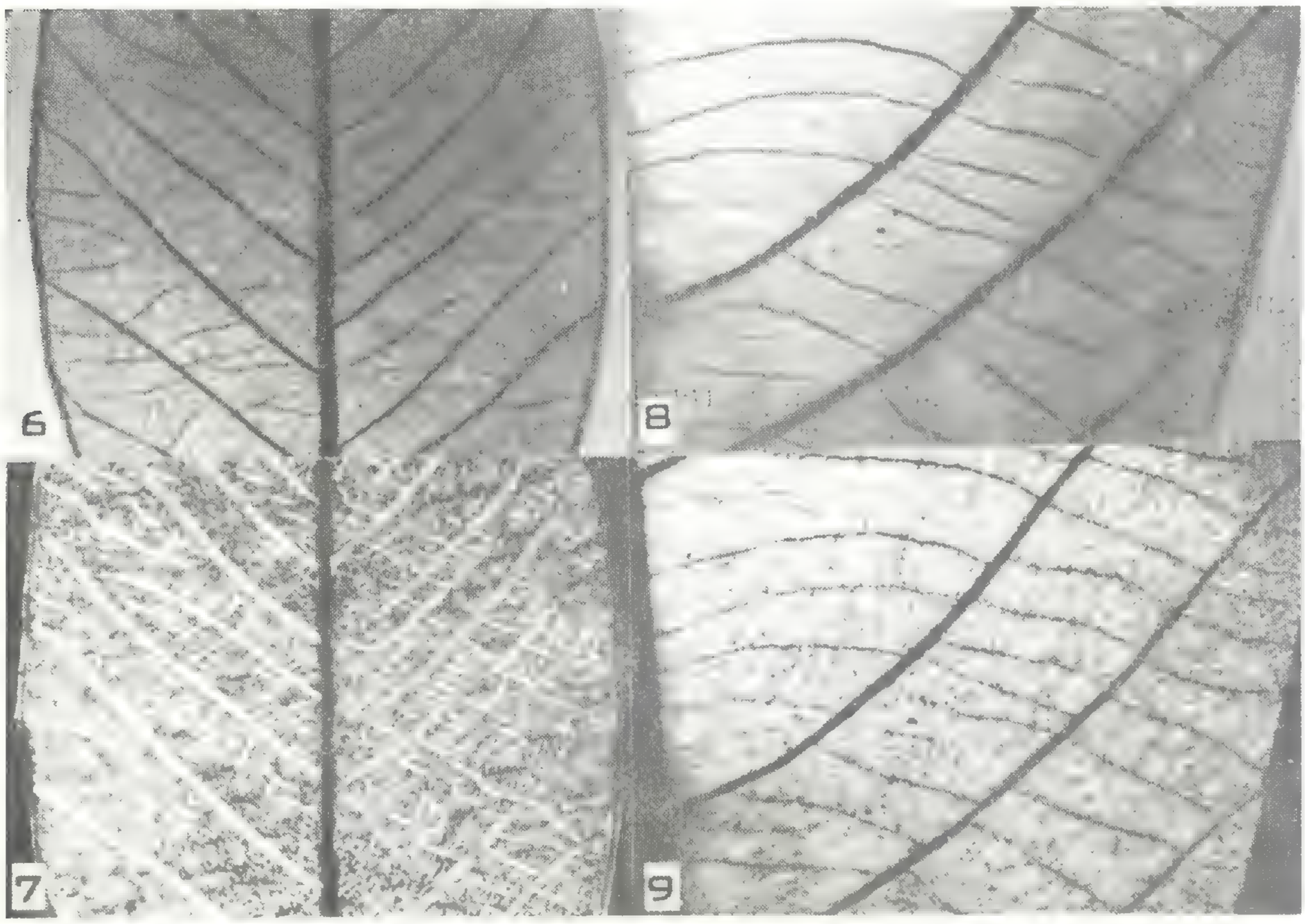


FIGS. 1–5. Cross sections of lower leaf epidermis of species of *Enkleia* including the stomatal apparatus. Guard cells (borne above the lower epidermis) are shown in cross section while the accessory cells (projecting below the lower epidermis) are shown in longitudinal section. Mesophyll and other leaf tissues are not illustrated. Note variation in the differentially thickened walls of epidermal cells. 1, *E. thorelii* (*Kerr 19930*); 2, *E. paniculata* (*Van Royen 3592*); 3, *E. malaccensis* (*Kostermans 7034*); 4, *E. siamensis* ssp. *siamensis* (*Poilane 14229*); 5, *E. siamensis* ssp. *andamanica* (*Parkinson 384*).

The pinnate venation is similar throughout the genus. The primary lateral veins number from nine to thirty-five per leaf. They are separated by a distance of several millimeters to a centimeter and a half (the distance between major veins appearing to be determined by leaf size). These veins are somewhat arcuate-ascending and end in a variously developed submarginal vein. Each vein is supported above and below by an extraxylary fiber sheath which is more extensive than the vein.

The secondary veins are numerous and generally form direct connections between adjacent primary veins. In the larger leaves, at least, these cross-connecting veins are almost at right angles to the costa. The pat-

tern thus formed is quite distinctive (FIGS. 6, 8). The secondary veins have a fiber sheath associated with them in the same manner as the larger veins. The xylem is very poorly lignified, and, in *Enkleia malaccensis*, I could perceive no color reaction when testing with phloroglucin and hydrochloric acid. The xylary elements, with the exception of the protoxylem, often have very thickened walls and reduced lumina. This peculiarity is discussed further in the paragraph on petiole structure.



FIGS. 6–9. Photographs of cleared leaves showing veins and associated fibers of two species of *Enkleia*. × 3. FIGS. 6, 7. *E. thorelii* (*Thorel 2823*); 6, with transmitted light showing venation pattern; 7, with polarized light showing venation pattern as outlined by the associated fibers. FIGS. 8, 9. *E. malaccensis* (*Griffith 4375*); 8, with transmitted light showing venation pattern; 9, with polarized light showing venation pattern and fibers not associated with the venation.

The extraxylary fibers accompanying the veins have very thick secondary walls. In prepared material, the secondary wall is usually pulled away from the thin primary wall. Concentric lamellations appear to be present in the secondary walls but should be studied further. The secondary walls react quite strongly with potassium iodide and sulphuric acid but give no reaction with phloroglucin and hydrochloric acid, thus indicating their cellulosic nature. These fibers, which appear superficially similar to the primary phloem fibers of *Cannabis* figured by Esau (*Pl. 24 A*), are intimately associated only with the veins in *Enkleia thorelii* (FIG. 7) and *E. siamensis* ssp. *siamensis*. In *E. siamensis* ssp. *andamanica* and *E. paniculata* a few of the fibers wander from the vein and intrude into adjacent tissues. The wandering of fibers reaches its zenith in *E.*

malaccensis where they are found in great profusion (FIG. 9). They apparently grow apically, often striking out vertically until reaching the upper or lower epidermis and then running horizontally. They can be observed readily in leaf sections and appear to be similar to the fibers described by Thoday (1921) in the African *Passerina filiformis* L. Near the veinlet endings in *E. thorelii* and *E. siamensis* ssp. *siamensis* the fibers are replaced by irregularly shaped sclereids. Sclereids also are found associated with the vein endings in *E. siamensis* ssp. *andamanica* and *E. paniculata* but are not as reduced as in the preceding two species. The situation in *E. malaccensis* could not be determined because of the too numerous wandering fibers.

Cross sections of the petiole were studied to check information given by Metcalfe and Chalk (1950) indicating the presence of intraxylary phloem in petioles of *Enkleia*. In all species of the genus the xylem, at midpetiole, is arc shaped. The arc often has strongly recurved ends and appears somewhat involute. The tracheary elements, except for the protoxylem but including the parenchyma, have curiously thickened walls and very reduced lumina. When stained with safranin and fast green, only the middle lamella appears to stain well with safranin but the entire wall can be weakly stained with phloroglucin and hydrochloric acid. No color reaction is formed with potassium iodide and sulphuric acid, probably indicating very weak lignification of the wall. Visually the walls appear to be rather similar to those of the extraxylary fibers. The greatest degree of thickening has taken place in *E. thorelii*. Phloem is found on both sides of the arc, confirming the statement of Metcalfe and Chalk, but the taxonomic significance of this is doubtful. Few to many scattered extraxylary fibers are found surrounding the trace, but the fibers are not nearly as prevalent as in the stem and leaf. The fibers have thick nonlignified cellulose walls.

Reproductive Morphology. The same terminology which I applied to the inflorescence in previous papers concerning the Thymelaeaceae (1959, 1961) is used here. The inflorescence is composed of the primary peduncle with a pair of bracts, a bracteole, a rachis, the secondary peduncles, and the flowers with their pedicels.

The floriferous branches of *Enkleia* are composed of many inflorescences which collectively appear to form a single, large, terminal inflorescence. The species of *Enkleia* (with the exception of *E. malaccensis*) bear their inflorescences in an axillary position on the terminal portions of young shoots. Each axillary inflorescence is simple, with the individual members cymosely arranged, i.e., opposite, except in very vigorous plants in which they become alternate by elongation of the internodes.

The floriferous shoots of *Enkleia malaccensis* are characterized by the development of several to many axillary branches which bear the individual inflorescences. The floriferous branches thus appear to be paniculiform. A few specimens of *E. siamensis* subsp. *siamensis*, such as *Poilane 14229*, also branch in this manner.

The reduced leaves subtending the axillary inflorescences are borne on the primary peduncle which they subtend; the trace initiation is, of course, below the point of external branching. Occasionally, this displacement is quite striking, as in *Zippelius 148a*. On one of the flowering shoots of this specimen the reduced leaves have been "carried out" onto the axillary shoots for about eight millimeters. The mechanics and meaning of this displacement are not entirely clear. It is interesting that the separation layer of the petiole appears to be forming at the point where the petiole and axillary branch fork. The entire pattern is essentially the same as that found in *Linostoma*.

Vegetative growth is resumed by the development of dormant axillary buds subtending the floriferous region of the shoot. The old inflorescences die shortly after fruiting and are soon broken off.

A single bracteole is borne at the apex of the primary peduncle. It is linear, to 8 mm. in length, and almost invariably persistent in fruit.

In addition to the bracteole, the primary peduncle bears a pair of bracts. In this genus the bracts are small and very strongly keeled until anthesis. At anthesis they are opposite or subopposite and are borne near or below the middle of the primary peduncle (*Enkleia paniculata* and *E. siamensis* ssp. *siamensis*), below the middle of the primary peduncle (*E. malaccensis* and *E. thorelii*), or above the middle of the primary peduncle (*E. siamensis* ssp. *andamanica*). Subsequently, they rapidly expand and become plane. A change in orientation generally accompanies the expansion, for the bracts are suberect prior to anthesis and then become deflexed, sometimes strongly so, in fruit. In addition, their position on the primary peduncle is radically shifted sometimes because of differential elongation of the axis. Elongation, during fruit maturation, takes place in all taxa except *E. siamensis* ssp. *siamensis* and is in striking contrast to the situation in *Linostoma* in which elongation is negligible. The function of the bracts is still an open question, as I suggested previously (1961), although Ridley (1930, p. 93) says, "When ripe the fruit on its peduncle, with the 2 bract leaves attached, separates from the plant and, rotating rapidly, drifts away in the wind across the forest to some distance, very much in the same way as the fruit of a Lime tree does." As in *Linostoma*, the separation layer occurs between the secondary peduncle and pedicel so that the chances of the drupe separating with the primary peduncle and its bracts seem slim.

Mature bracts are elliptic to obovate in shape and are quite unlike the foliage leaves. In addition to shape, the bracts are dissimilar in other respects, namely, smaller size, lighter color, thinner texture, and more reticulate venation. The venation pattern is essentially the same as that of the leaf (particularly with respect to the orientation of secondary veins). The individual veins, however, tend to be larger, giving a more thickly veined aspect to the bracts. The submarginal vein is well developed in *Enkleia siamensis* but poorly developed in *E. paniculata* and *E. malaccensis* (*E. thorelii* not determined because of insufficient material).

A study of the anatomical characteristics of the bract, based on cross sec-

tions, was not pursued, except in *Enkleia malaccensis*, because of the difficulty in obtaining satisfactory results. The bracts from herbarium specimens re-expand poorly because of the large number of thin-walled cells. The epidermal cells lack the extreme thickening found in the leaves, but the stomatal distribution is the same (i.e., on the abaxial surface only). The stomatal structure, however, is modified and is discussed below. Since extreme crushing and distortion were found in the mesophyll, no observations could be made on this tissue. The veins have the usual fibers associated with them. In *E. siamensis* and *E. paniculata* the outermost fibers of the fiber sheath are modified into shorter sclereids which have one wall conspicuously enated as in *Linostoma*, but in *E. malaccensis* this does not occur. As might be expected the fibers in the bracts of *E. malaccensis* and *E. paniculata* wander from the veins just as in the leaves of these species. The bract petiole is enervated by a single arc-shaped trace with strongly inrolled margins. All cells with the exception of phloem cells embraced by the arc are heavily sclerified. Extraxylary fibers do not appear to be present.

The stomatal structure is superficially dissimilar in leaf and bract. In the bract, the numerous accessory cells are fewer in number (generally four to eight), and they retain the tabular form which characterizes the surrounding epidermal cells. Thus, the stoma is not borne within a substantial pit. I believe that this indicates the pit-type (as found in leaves of all *Enkleia* species and *Linostoma decandrum*) to be much more closely related to the ranunculaceous type (as in *L. persimile* and *L. pauciflorum*) than might be expected. It indicates also the need for ontogenetic studies of the stomatal differentiation to determine the sequence of divisions in the formation of the pit-type. Unfortunately, small leaves from herbarium specimens are too difficult to handle because of brittleness and pubescence to permit such a study, even if sufficient material was available.

The flowers are arranged on the rachis in an indeterminate manner (the lowermost flower being the first to bloom). The flower clusters are umbelliform to subracemiform, depending on the length of the rachis. The form of the flower cluster is somewhat static within the species, but it is not considered to be a dependable taxonomic character. The number of flowers per inflorescence varies from three to sixteen in *Enkleia siamensis*, with the range of variability of other species falling within this number.

The flowers are bisexual, regular, pentamerous, perigynous and pedicellate. The terminology applied to the parts is the same as used in my previous papers concerning the family (1959, 1961). Further gross morphological information concerning the flower, beyond that presented in the following discussion, may be found in the specific descriptions.

The calyx tube, as in other members of the family, is composed of the fused bases of calyx, corolla, and androecial members. It is tubular in all species except *Enkleia malaccensis* in which it varies to suburceolate. The exterior is variously pubescent; the pubescence in all cases is minute. The interior is glabrous in all species, except *E. malaccensis* in which the tube interior is completely glabrous, or villous above and glabrous below, or

completely villous. The trichomes are exclusively unicellular and unbranched.

The tube is vascularized by ten distinct veins which are marked externally by inconspicuous ridges. Five of the traces are in the antisepalous position (median traces) and five are in the alternisepalous position (each consisting of a fused pair of traces designated as commissural traces). Occasional branching of a main trace occurs, but these branches usually reunite with the parent trace. Approximately half way up the tube the traces to the alternisepalous stamens depart from the commissural traces and shortly thereafter the traces to the antisepalous stamens depart from the median traces. In *Enkleia siamensis* each commissural trace and median trace gives rise to two lateral traces slightly above the insertion of the alternisepalous stamens. These lateral traces fuse (i.e., one of commissural origin with one of median origin) forming an inverted "V" pattern lying between the main traces. At the apex of this inverted "V" a trace is formed which contributes eventually to the vascularization of the calyx lobes. The commissural traces then dichotomize giving rise to the two lateral calyx lobe traces, and the median traces continue undivided as the calyx lobe median traces. In *E. thorelii* and *E. paniculata* a minor deviation from this pattern is found. The median trace gives off a pair of lateral traces in the same position and manner as in *E. siamensis*, but the corresponding lateral traces from the commissural traces are not formed. The laterals (from the median trace only) thus do not form the inverted "V" pattern but fuse directly with the commissural traces. This pattern appears similar to that demonstrated by Heinig (1951, *Fig. 56*) in *Pimelea prostrata*, except that in *Enkleia* the commissural traces are fully developed for the entire length of the tube.

The size and shape of the five calyx lobes vary insignificantly among the species. The lobes are vascularized by three or five main veins which send off numerous branches which anastomose repeatedly. As in *Linostoma*, the aestivation of the lobes is quincuncial.

The petals are inserted at the orifice of the calyx tube in an alternisepalous position and are erect and glabrous in all species. They are divided medially either completely or incompletely. The median division is incomplete in *Enkleia paniculata* and *E. malaccensis* but complete in *E. siamensis*, and *E. thorelii*. The shape of the lobes is ensiform (*E. paniculata*), linguiform (*E. malaccensis*), or liguliform (*E. siamensis* and *E. thorelii*).

The petals can be interpreted in two conflicting ways depending on the supposed origin of these structures. Heinig supports the hypothesis that the structures are stipular in nature (see her 1951 publication for comprehensive discussion), while I support a petalaceous origin (1960, 1961). It is, admittedly, easier to explain the various types found within the family on the basis of her hypothesis but I feel that an attempt to gain information in support of the other view must be made. I interpret the incomplete division of the lobes as primitive and the complete division of the lobes as advanced (Heinig's position would be quite the opposite).

Only the petals of *Enkleia thorelii* have any hint of vascularization. I found one petal lobe which was vascularized for about one-third its length, the vascularization consisting of a single trace at most three tracheids in diameter and with a few accompanying fibers. Several other lobes bore a few fibers in the position that vascularization would be expected. I interpret the presence of these fibers as indicating a degeneration of a previously existing vascular system. The vascular supply of the single lobe and the fibers of several additional lobes appear to arise from the lateral calyx lobe trace.

The androecium consists of ten stamens inserted on the calyx tube. They are in two whorls, the upper whorl in the antisepalous position and the lower whorl in the alternisepalous position. The traces which supply the stamens reflect the external position of the stamens in that they also depart from their parent traces in two distinct whorls.

The filaments are short (to 1 mm. long), stout, and slightly inflated just below the anther. They are glabrous except in some specimens of *Enkleia paniculata* in which a few trichomes may be present at the base of the anther. Vascularization is by a single bundle which either ends at the base of the connective (*E. siamensis* and *E. malaccensis*) or extends to the very distal portion of the connective (*E. paniculata* and *E. thorelii*).

The antisepalous anthers are exserted or subexserted, except in *Enkleia siamensis* ssp. *andamanica* where they are included. Alternisepalous anthers are included except in *E. paniculata* in which they are subexserted. They are 4-lobed and 4-loculed in cross section. Dehiscence is longitudinal. There is some basal inflation of the connective but not nearly so pronounced as in *Linostoma*. The connective is minutely produced beyond the pollen sacs and, on the basis of cell shape and size, may be glandular in function.

The pollen of the four species is, for all practical purposes, uniform. It is polyporate and highly sculptured. It cannot be distinguished from the pollen of *Linostoma*.

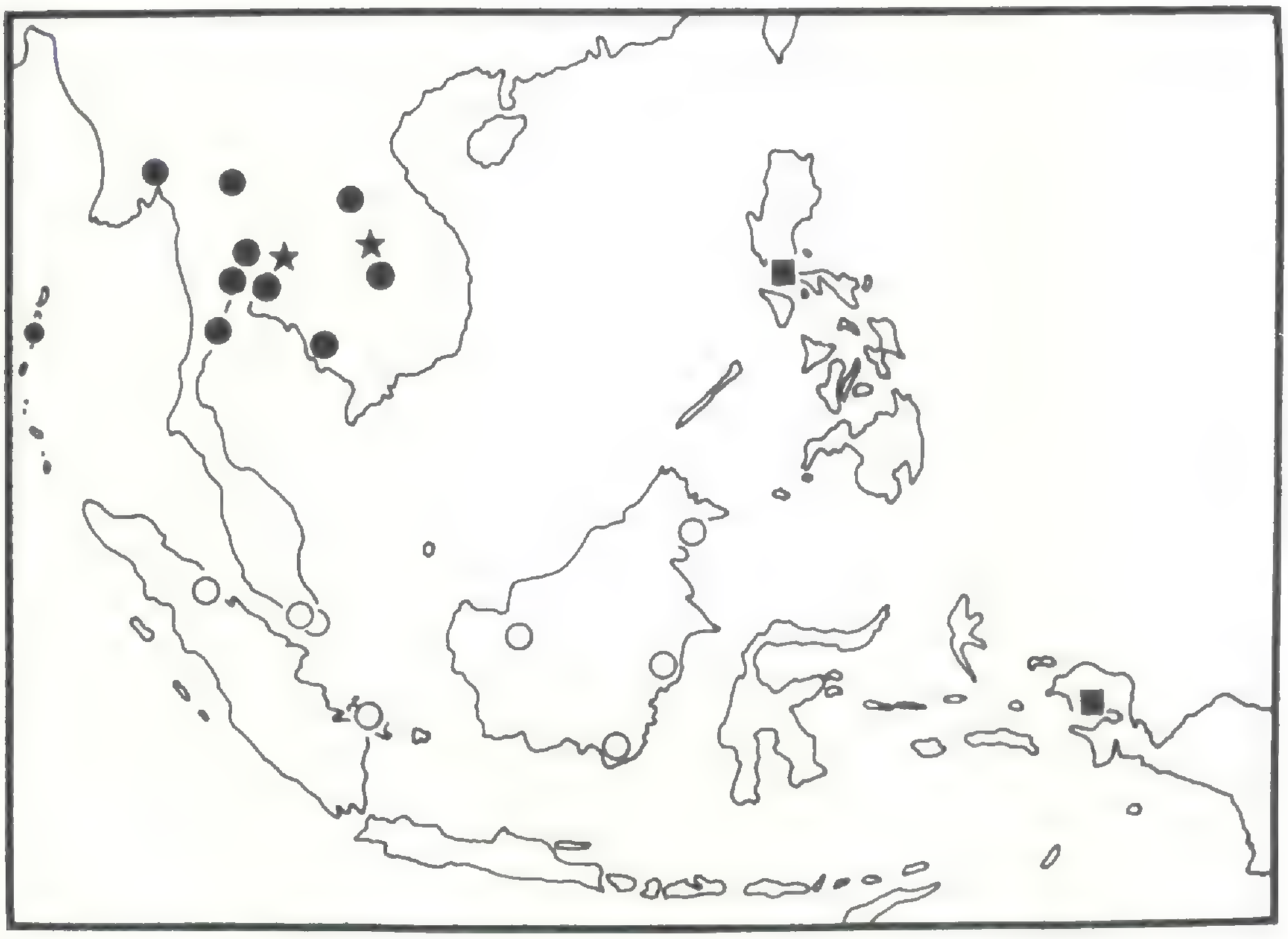
The disc is borne at the base of the calyx tube. It consists of minute free lobes in *Enkleia siamensis* and *E. thorelii*, while in *E. paniculata* it is basally adnate to the calyx tube. No vascularization is present. The disc in *E. malaccensis* is completely adnate and amounts to only a few additional cells in the thickness of the calyx tube wall. It is regularly lobed with the apex of each lobe coinciding with one of the main veins of the tube.

The gynoecium is composed of a single pistil, presumably of the pseudomonomeric type. It is sessile or nearly so. I have found it impossible to clear the gynoecium satisfactorily, even when placed in clearing agents for greatly extended periods of time, so that vascular patterns could not be established.

The style is borne terminally on the ovary. It is filiform, glabrous, and sometimes variable in length. Style length in comparison to ovary length has been used in the past as a character to separate *Enkleia* and *Linostoma*. An evaluation of this character is made in the discussion of *E.*

siamensis. The stigma is subcapitate in *E. paniculata* and *E. siamensis* but clavate in *E. malaccensis* and *E. thorelii*.

As in *Linostoma*, the drupes of *Enkleia* are preserved poorly and I do not feel that I can comment upon them. The calyx tube is persistent but not accrescent. It is longitudinally ruptured by the developing drupe in *E. malaccensis* but transversely ruptured in *E. paniculata* and *E. siamensis* (see also discussion following *E. paniculata*). The fruit of *E. thorelii* is unknown at this writing.



Distribution of the species of *Enkleia:* squares, *E. paniculata;* circles, *E. malaccensis*; large solid dots, *E. siamensis* ssp. *siamensis*; small solid dot, *E. siamensis* ssp. *andamanica*; stars, *E. thorelii*.

GEOGRAPHY

The four species of *Enkleia* have a composite range extending from Burma, Thailand, and Cambodia, on the north, through the Malay Peninsula, Andaman Islands, and Sumatra to Bangka, on the south, eastward through Borneo to western New Guinea and the Philippine island of Luzon. The distribution is strongly correlated with specific delimitation with the exception of *E. paniculata*. The disjunct distribution of the latter species (Luzon and western New Guinea) is puzzling indeed, but the species is represented so poorly in herbaria that additional collections may show this disjunction to be an artifact.

The distribution of each species is shown on the accompanying map. The symbols indicate place of collection only and are in no way indicative of the relative frequency of the plants.

MATERIALS

This revision is based on specimens from the following herbaria, the abbreviations for which are taken from Lanjouw & Stafleu's *Index Herbariorum, Part I*, Ed. 4 (Regnum Vegetabile, 15. 1959).

A Arnold Arboretum of Harvard University, Cambridge
BM British Museum (Natural History), London
C Botanical Museum and Herbarium, Copenhagen
DD Forest Research Institute & Colleges, Dehra Dun
F Chicago Natural History Museum, Chicago
G Conservatoire et Jardin botaniques, Genève
GH Gray Herbarium of Harvard University, Cambridge
K Herbarium, Royal Botanic Gardens, Kew
L Rijksherbarium, Leiden
P Muséum National d'Histoire Naturelle, Paris
US U. S. National Museum, Smithsonian Institution, Washington

I wish to take this opportunity to thank the directors and curators of the above institutions for allowing me to examine the specimens in their care. I also wish to thank, in particular, Drs. C. E. Kobuski, C. E. Wood, Jr., and O. T. Solbrig for unfailing interest, constructive advice and technical assistance.

TAXONOMY

Enkleia Griffith, Calcutta Jour. Nat. Hist. 4: 234. 1844 (TYPE: *E. malaccensis* Griffith).

Linostoma subg. *Linostoma* Kurz, Jour. As. Soc. Bengal **39**(2): 83. 1870, as to species cited.

Macgregorianthus Merrill, Philippine Jour. Sci. 7: 312. 1912 (TYPE: *M. paniculatus* Merrill).

Erect or scandent shrubs or lianas, the axillary branches sometimes modified for climbing, the bark containing many fibers. Leaves opposite, subopposite, or rarely alternate, simple, pinnately veined, the primary lateral veins arcuate, with numerous oblique secondary veins; entire, petiolate, estipulate. Inflorescences laxly clustered towards the apex of the young shoots, the bracts small and keeled at anthesis, becoming plane and much enlarged in fruit, the primary peduncle generally elongating following anthesis. Flowers bisexual, pentamerous, perigynous; calyx tube tubular, nonarticulated, ribbed, variously pubescent; calyx lobes 5, quincuncial, spreading; petals 5, medially cleft to the base or nearly to the base, inserted alternisepalously at the orifice, the lobes ensiform, linguiform or liguliform, glabrous; stamens 10, inserted in 2 whorls, the upper whorl antisepalous, the lower whorl alternisepalous, the anthers short filamented, basifixed, longitudinally dehiscent, the connective minutely produced beyond the pollen sacs; disc of irregular lobes, minute, free to adnate to the calyx tube; gynoecium single, pseudomonomeric, superior,

unilocular with a single anatropous ovule, the style terminal, the stigma clavate or subcapitate. Fruit drupaceous, the calyx tube variously ruptured by the developing drupe.

KEY TO THE SPECIES

a. Leaf surface at most minutely puberulent, often glabrescent beneath, the trichomes short, straight, at most suberect; calyx tube becoming spirally twisted in the upper half before being transversely ruptured by the developing drupe; petals cleft nearly to the base; alternisepalous stamens subexserted. ..... 1. *E. paniculata.*

a. Leaf surface tomentulose, velutinous, glabrescent or glabrous beneath, the trichomes of medium length, curly or at least curved, suberect to erect; calyx tube never twisting before being transversely or longitudinally ruptured by the developing drupe; petals cleft to the base or nearly to the base; alternisepalous stamens included.

b. Erect shrubs, scramblers or lianas; leaves tomentulose, velutinous, glabrescent or glabrous beneath; inflorescence umbelliform; calyx tube 5–8 mm. long; ovary densely sericeous.

c. Primary lateral veins 10–15 pairs per leaf; calyx tube glabrous, partially or completely villous within, longitudinally ruptured by the developing drupe; petals cleft nearly to the base, about 1 mm. long; antisepalous stamens exserted; disc completely adnate to the calyx tube. ..... 2. *E. malaccensis.*

c. Primary lateral veins 20–35 pairs per leaf; calyx tube glabrous within, transversely ruptured by the developing drupe; petals cleft to the base, 2–2.5 mm. long; antisepalous stamens included to subexserted; disc free. ..... 3. *E. siamensis.*

b. Erect shrubs, usually low; leaves glabrous beneath; inflorescence subracemiform; calyx tube 6–11 mm. long; ovary sparsely sericeous. ..... 4. *E. thorelii.*

1. **Enkleia paniculata** (Merrill) Hallier f. Med. Rijksherb. **44:** 26. 1922.

Macgregorianthus paniculatus Merrill, Philippine Jour. Sci. **7:** 312. 1912 (TYPE: *McGregor B.S. 12360!*).

Enkleia zippeliana Hallier f. Med. Rijksherb. **44:** 26. 1922 (TYPE: *Zippelius 148a!*).

Climbing shrubs or lianas; young stems minutely ochraceous-velutinous and glabrescent, reddish brown, the lenticels conspicuous, horizontally elongate. Leaves opposite, subopposite or alternate; leaf blades ovate to elliptic or oblong-elliptic, 4–11 cm. long, 2.5–6 cm. broad, acute to obtuse at the apex, obtuse at the base, subcoriaceous, minutely and sparsely puberulent, often glabrescent, slightly darker above than beneath, the costa plane to immersed above, elevated beneath, the primary lateral veins 9–20 pairs, the submarginal vein coinciding with the margin; petiole terete or nearly so, 3–9 mm. long, minutely puberulent or velutinous. Inflorescences borne terminally on the young stems, usually 15–45 cm. long, many nodes involved, minutely velutinous throughout; each inflorescence

5–12-flowered, subumbelliform, the primary peduncle 2–3.5 cm. long, enlarging to 6 cm. in length with most of the elongation above the insertion of the bracts, usually bearing the reduced leaf of the subtending node near the base, the rachis 1–2 mm. long, the secondary peduncles to 2 mm. long, the bracts at anthesis opposite or subopposite, borne near the middle of the primary peduncle or below, keeled, small, minutely velutinous, suberect, the bracts in fruit becoming plane, narrowly elliptic, 5 6.5 cm. long, blunt at the apex, obtuse to subcordate at the base, membranaceous, deflexed, the bracteole borne near the summit of the primary peduncle, linear, 2–5 mm. long, persistent. Calyx tube tubular, 5.5–6.5 mm. long, 1–1.5 mm. in diameter at the orifice, minutely puberulent without, glabrous within; calyx lobes ovate, 2–2.5 mm. long, 1–1.25 mm. broad, minutely but densely puberulent within, erect; petals cleft nearly to the base, the lobes ensiform or when immature erosely truncate, ca. 1 mm. long, glabrous, erect; stamens inserted in two whorls, the antisepalous whorl inserted just below the petals, exserted as far as the petal apices, the alternisepalous whorl inserted about one anther's length below the antisepalous one, subexserted, the anthers oblong, 0.5–1 mm. long, 0.25 mm. broad, the filaments 0.25–0.75 mm. long, thick, glabrous or with a few minute trichomes near the base of the anther; disc of minute, irregular lobes, adnate to the calyx tube; ovary ellipsoid, densely short-sericeous, the style terminal, filiform, ca. 2 mm. long, glabrous, the stigma subcapitate, papillose; pedicel 2.5–5.5 mm. long, greatly thickening in fruit. Only one fruit per inflorescence developing; calyx tube spirally twisting before being ruptured by the developing drupe, torn portions persistent at the base; drupe ovoid to ellipsoid, ca. 1.5 cm. long, 1 cm. in diameter, sericeous, becoming glabrescent.

ILLUSTRATION. Thymelaeaceae. *In:* Flora Malesiana I. 6: 1–48, *fig. 10, h,i.* 1960.

DISTRIBUTION. Collected only three times, once on Luzon and twice in western New Guinea. The McGregor collection from Luzon was found "on forested slopes at low or medium altitudes." This collection was made in December when the plant was beginning to flower. The Van Royen collection from New Guinea was made in December in flower and fruit. Van Royen wrote of the locality, "The area in which the species is found consists of elevated limestone cliffs, alternating with brown muddy swamps." [1] He says, in addition, "I am quite surprised that my collection of this species is only the second one as this species was really common where I found it. I had to scale a relatively steep slope covered with an open forest of Quercus sp. and Pometia as the dominating trees. This Enkleia was climbing on an Artocarpus vrieseanus Miquel, but was found climbing also over Paratrophis sp., Cyathocalyx papuanus Diels and over both Quercus and Pometia. It is a rather striking species owing to its relatively large flowers."

[1] Personal communication.

Philippine Islands. LUZON: Calauan, Prov. of Laguna, *McGregor B.S. 12360* (K-lectotype, BM, L, US). **Netherlands New Guinea.** Steenkool, road to Temboeni, km. 1.5, hills east of the road, opposite police barracks, *Van Royen 3592* (L); without locality, *Zippelius 148a* (L-holotype and isotoypes of *E. zippeliana*).

Presumably, the holotype of this species was destroyed with the Philippine National Herbarium. As lectotype I choose the specimen of *McGregor 12360* deposited in the herbarium at Kew. It is the most complete specimen of this collection and consists of two immature floriferous branches and a packet containing a nearly mature flower.

Merrill allied his new genus *Macgregorianthus* with *Wikstroemia*, a large and wide-ranging genus of the Eastern Hemisphere. He placed it near this genus, undoubtedly, because of his familiarity with it rather than because of any morphological similarities. There is no question that *Macgregorianthus* (= *Enkleia*) is not closely related to *Wikstroemia*, although they are members of the same subfamily.

The calyx tube, immediately following anthesis in the New Guinea specimens, becomes spirally twisted in the upper half. It twists, up to a half dozen times, quite tightly before being ruptured by the developing drupe. The twist is invariably counter clockwise. The significance of this peculiar behavior has not been ascertained.

Enkleia paniculata was first united with *E. zippeliana* shortly after Hallier's description of the latter species. Hou recently (1960) pointed out that the distinguishing features mentioned by Hallier in the original description of *E. zippeliana* are of little taxonomic consequence. These features include leaf pubescence, pubescence color and prominence of leaf venation.

There is, however, a discrepancy in one major floral character which requires explanation. The flowers of the New Guinea specimens collected by Zippelius and Van Royen have petal lobes which are ensiform, whereas, the McGregor collection consisting of immature flowers has petal lobes which are broadly squamelliform with the apices erosely truncate. The petals have not fully developed in the McGregor specimens. Fortunately, the superb Van Royen collection consisting of flowering and fruiting material is available so that immature flowers can be compared with those of the Luzon collection. In buds of comparable size to those of the McGregor collection, the petal lobes have already undergone major elongation and they have assumed the mature form, but in somewhat younger buds the erosely truncated petal apices so characteristic of the Luzon collection can be observed.

Cleared leaves of the New Guinea specimens have a remarkable number of druse-like crystals which can be observed readily under low magnification. The leaf specimen of *McGregor 12360* which I cleared was absolutely devoid of crystals. The applicability of this character is very doubtful as crystal formation may be due to the physiological state of the plant at the time of collection and not directly genetically controlled. Indeed, in *Enkleia malaccensis* crystals can be found in the leaves of most

of the specimens but are entirely lacking in others, *Griffith 4375*, for example. Since all of the leaves were handled in a similar manner there is little chance that crystal formation was induced by the clearing process in some instances and not in others.

2. **Enkleia malaccensis** Griffith, Calcutta Jour. Nat. Hist. **4**: 234. 1844 (TYPE: *Griffith ?*).

Lasiosiphon scandens Endl. Gen. Suppl. **4**(2): 67. 1847, based on *Enckleia* [*Enkleia*] *malaccensis* Griffith.
Enkleia malayana Griffith, Notul. As. **4**: 363. 1854.
Linostoma scandens (Endl.) Kurz, Jour. As. Soc. Bengal **39**(2): 83. 1870.
Enkleia riouwensis Hallier f. Med. Rijksherb. **44**: 25. 1922 (TYPE: *Teysmann s.n.*!).
Enkleia coriacea Hallier f. *Ibid.* (TYPE: *Hallier B.2264*!).

Climber; young stems terete, densely golden-brown velutinous, gradually glabrescent and conspicuously lenticellate, reddish brown; axillary branches often strongly recurved uncinate, thickening at the base with age. Leaves subopposite, the blade ovate to elliptic (sometimes broadly so), 3.5–14(–15) cm. long, 2–7(–10) cm. broad, acute to obtuse or emarginate or rarely short-acuminate at the apex, cuneate to obtuse at the base, coriaceous, both surfaces golden-brown velutinous and glabrescent, the trichomes slightly curved, the costa immersed above, elevated beneath; the primary lateral veins 10–15 pairs, the submarginal vein coinciding with the margin, conspicuously thickened; petiole terete, densely puberulent although somewhat glabrescent in very old leaves, 6–10(–12) mm. long. Inflorescences borne terminally on the young shoots, involving several nodes, generally compound and forming a paniculate structure often 15 cm. long but sometimes to 30 cm. in length, golden-velutinous throughout; each inflorescence 3–9-flowered, umbelliform, the primary peduncle 3–5 cm. long, enlarging to 9 cm. in fruit with most of the elongation above the insertion of the bracts, usually bearing the very reduced leaf of the subtending node near the base, the rachis to 2 mm. long but sometimes elongating in fruit, the secondary peduncles obsolete to 2 mm. long, the bracts at anthesis subopposite, borne slightly below the middle of the primary peduncle, keeled, 3–5 mm. long, golden-brown velutinous, erect, the bracts in fruit becoming plane, elliptic to obovate 4–7 cm. long, 1–2.5 cm. broad, obtuse at the apex, subtruncate at the base, puberulent, conspicuously veined, strongly deflexed, the bracteole borne at the summit of the primary peduncle, linear, 1–3 mm. long, often persistent. Calyx tube tubular to suburceolate, 5–6 mm. long, green to yellow and densely golden-brown velutinous without, glabrous, villous above and glabrous below or completely villous within; calyx lobes more or less oblong but obtuse at the apex, 1–2 mm. long, 0.75 mm. broad, erect, white puberulent within; petals cleft almost to the base, the lobes somewhat linguiform, ca. 1 mm. long, somewhat carnose, glabrous, exserted; stamens inserted in two whorls, the antisepalous stamens inserted just below the petals, exserted

but not as far as the petals, the alternisepalous stamens inserted one to two anther-lengths below the antisepalous whorl, included, the anthers oblong, 0.5–1 mm. long, 0.25–0.5 mm. broad, the filaments obsolete to 0.5 mm. long, slightly inflated just below the anthers, glabrous; disc completely adnate to the calyx tube, ca. 0.5 mm. tall, somewhat fleshy; stigma included, clavate, papillose; style filiform, 0.5–1 mm. long, the ovary fusiform, ca. 2 mm. long, densely short-sericeous; pedicel 1–3 mm. long. Usually only one or rarely two fruits per inflorescence developing; calyx tube persistent, usually longitudinally ruptured and persistent at the base of the drupe; drupe ovoid, 10–15 mm. long, 6–8 mm. in diameter, glabrescent but usually puberulent at least at the apex, prominently ribbed; pedicel thickening in fruit.

ILLUSTRATIONS. Ridley, H. N., Dispersal of plants throughout the world. *tab. 6, fig. 13*, L. Reeve & Co., Ltd., 1930; Thymelaeaceae. *In:* Flora Malesiana I. 6: 1–48. *fig. 10, a–g*. 1960.

DISTRIBUTION. Primary forest in Malaya, south to Sumatra and Bangka, east to North Borneo. All specimens which I have seen indicate that this species is never found above 50 meters altitude. It has been collected flowering in April, September and October; fruiting in April, May, August and September. Merrill (1929, p. 212) says, "A woody vine forming tangled masses in forests, the stems a few inches in diameter." Keith reports that the bast fibers can be used for tying purposes, and Burkill (1935, p. 925) says that it yields an inferior aromatic wood.

Malaya. MALACCA: Malacca, *Griffith* "1845" (K). LOCALITY UNCERTAIN: Sungei Hudacely, *Ridley 1764* (BM); *Griffith E.I.C. 4375* (GH, K). **Singapore.** Buket Temah, *Ridley 6427* (BM); Garden Jungle, *Ridley 5565* (BM); south side of MacRitchie Reservoir, *Sinclair SFN 40694* (K); *Maingay 1308 2* (BM, GH, K, L); without collector (possibly Maingay?) *1256* "Sept. 1867" (G). **Indonesia.** SUMATRA: Laboehan Batoe; Dist. Kota Pinang, Si Mandi Angin (on the Soengei Kanan), *Toroes 4099* (A). BINTAN: Tandjung-Pinang, *Teysmann s.n.* (L-holotype and isotoype of *Enkleia riouwensis*). BANGKA: G. Maroe, *Anta 1373* (A). BORNEO: Tandjong Bangko region, near mouth of Mahakam river, *Kostermans 7034* (L); Loa Djanan, west of Samarinda, *Kostermans 6672* (L); Pleihari [Pelaihari], *N.I.F.S. bb. 19256* (A, L); zwischen dem Súngai Djĕmĕlá und dem Gûnŭng K(e)lamm, *Hallier B.2264* (L-holotype and isotype of *Enkleia coriacea*). **British North Borneo.** EAST COAST: Selangan, F.R., Semporna, *Keith N.B.F. D.N. 9234* (K, L); Tawao [Tawau], Elphinstone Province, *Elmer 20834* (BM, C, L).

It appears that a type specimen has never been selected for this species, although I have seen several specimens which have been considered by others to be type material. This species was described by Griffith (1844) in an article entitled, "On some remarkable Plants in the H. C. Botanic Gardens, Calcutta." However, immediately preceding the description of *Enkleia* (p. 234) he says, "The other plants of this family that I have met with on the N. E. frontier and Straits of Malacca, localities that, however distant, present remarkable affinities in vegetable forms, are–."

Enkleia malaccensis is the last of nine species in a list and it is marked clearly from "Malacca." The actual description is contained in an extensive footnote in which no specimen was selected as a type. Thus, it would seem that a selection of a type would be restricted to specimens collected by Griffith (or one of his collectors) in Malacca prior to 1844 but, as I intend to show, the selection of a type is relatively complicated.

Griffith first set foot in Malacca in August, 1841 (see Van Steenis-Kruseman, pp. 201, 202. 1950), and served as a civil surgeon until mid-1842. During this period he made collections and trained native collectors. In August of 1842 (see Griffith 1847, introductory notes) he left to assume the directorship of the Botanic Gardens in Calcutta, a post which he occupied until December, 1844. In January of 1845 he returned to Malacca. Of no little consequence is that during his directorship at Calcutta he remained in contact with his native collectors in Malacca and they sent him a steady stream of dried specimens, seeds, and living plants. The living plants were grown in the gardens (see Griffith, 1847, Extract of Letters).

One would assume from the title of Griffith's paper that the plants which he intends to discuss are growing in the botanic garden until he adds the qualification that he has met some of them elsewhere. In the case of the locality of this particular species I believe that it can be interpreted in two ways: one, the description is based on a plant which he collected in Malacca between August, 1841, and August, 1842; or two, the description is based upon a specimen growing in the botanic garden which was sent from Malacca by his collectors, but which may have been a plant with which he had familiarity prior to leaving Malacca. If the description is based upon one of his Malaccan collections there is a possibility that the specimen did not go through his normal channels of distribution, for, in a letter to R. Wight, postmarked Malacca, April 15, 1842 (Griffith 2: xxvii) he says, "I intend adopting an entirely new system of tactics, and when I pounce on any thing interesting, to keep it until it is in print." On the other hand, if the description is based upon a living specimen there is the distinct possibility that no herbarium specimen was made. As an example, in the same letter quoted above, he says, of three new genera, "which I suppose no body will adopt at home without specimens."

I have seen three specimens which have been considered to be authentic collections. Two of these are deposited at Kew. The one bears the stamp of "Herbarium Hookerianum, 1867," and in longhand is written, "Malacca, Griffith, 1845. Enkleia Malaccensis Griffith;" the other bears the same stamp of Hooker, plus the printed label of the East India Company with the identification number 4375 (see Hooker, 1865), and is identified as "Lasiosiphon scandens, Endl." (a substitute name for *Enkleia malaccensis*), the place of collection is given as "Birma and Malay Peninsula." In addition, it bears the longhand identification "Enkleia Malayana Gr." The third sheet, desposited at the Gray Herbarium, bears the identical East India Company label and identification as the Kew specimens but has no other marks. There is little question that all of

these sheets are Griffith collections but the sheet at Kew bearing the date 1845 is automatically eliminated as authentic type material. The remaining two sheets cannot be either confirmed or denied as type material. Griffith's description of the new genus is lengthy, well drawn, and easily interpreted so that I believe that the choice of a type should be left an open matter at this time.

Enkleia coriacea, on first examination, appears to be a distinct species. The aspect of the two Leiden specimens which seem to set them apart from others is due to a decidedly reddish cast to the leaves which is coupled to an almost complete lack of pubescence. It is surprising how this combination of characters is so readily noticeable. On very immature leaves the characteristic pubescence of *E. malaccensis* can be observed but the trichomes are shorter than usual. It is possible that these two specimens show one extreme of the total variation in trichome length of the species. The trichomes of other Bornean specimens in general appear to be shorter than those of peninsular specimens but none reach the extreme attained in *Hallier B.2264*. It is of interest that these plants were growing in association with *Linostoma pauciflorum* Griffith, a species of the genus most closely related to *Enkleia*.

Enkleia riouwensis was described by Hans Hallier from sterile collections of Teysmann from the Riouw island of Bintan. Hou (1960), in his treatment of Thymelaeaceae for the *Flora Malesiana*, relegated this species to the synonymy of *E. malaccensis*, an action with which I agree. I have examined the holotype and an isotype from the Leiden herbarium and can find no characteristics to distinguish it from *E. malaccensis*, except a more pronounced undulation of the leaf margin which may be due to the method of drying. In the description, Hallier refers to the plants as shrubs but I can find no such information on the two specimens which I examined, so I regard this character as questionable.

3. **Enkleia siamensis** (Kurz) Nevling, comb. nov.

Linostoma siamense Kurz, Jour. As. Soc. Bengal **39**(2): 82. 1870 (TYPE: *Teysmann 5986*!).

Erect to scrambling shrubs or large lianas; young stems terete, puberulent or golden to light-brown velutinous, glabrescent; axillary branches usually normal, only rarely becoming uncinate. Leaves opposite, subopposite or rarely alternate on vigorous young shoots; leaf blade ovate, lanceolate, oblong-elliptic, broadly elliptic or rarely orbicular, 4–13 cm. long, 2–9 cm. broad, acute, attenuate, or obtuse to truncate and minutely mucronulate at the apex, cuneate to obtuse at the base, coriaceous, glabrous or densely to sparsely tomentulose and often glabrescent, the trichomes curly, the costa immersed above, elevated beneath, the primary lateral veins 20–35 pairs, the submarginal vein poorly or well developed, coinciding with the margin; petiole scarcely canaliculate, glabrous or velutinous, 5–8 mm. long. Inflorescences borne on the modified portions of the young shoots, involving several nodes (to as many as 8), the main

axis seemingly leafless, to 15(–30) cm. long, minutely golden-velutinous throughout; each inflorescence 3–16-flowered, umbelliform, the primary peduncle 2.5–5 cm. long, sometimes elongating to 9 cm. in fruit, with the reduced leaf of the subtending node near the base, the rachis to 2 mm. long, the secondary peduncles to 1 mm. long, the bracts opposite to subopposite, keeled at anthesis, becoming plane and more or less oblong, 2–9 cm. long, 1–2.5 cm. broad, obtuse at the apex, obtuse to subcordate at the base, membranaceous, tomentulose, deflexed, the bracteole borne at the summit of the primary peduncle, linear, 1–8 mm. long, often persistent. Calyx tube tubular, 5–8 mm. long, 1–1.5 mm. in diameter at the orifice, golden-tomentulose without, glabrous within; calyx lobes spathulate, 2.5–4.5 mm. long, 1.5–2.5 mm. broad, minutely puberulent within, spreading; petals cleft to the base, the lobes liguliform, ca. 2.5 mm. long, glabrous, fleshy, long-exserted; stamens inserted in two whorls, the antisepalous whorl inserted just below the petals to 1 anther-length below, subexserted or included, the alternisepalous whorl inserted 2–3 anther-lengths below the antisepalous whorl, included, the anthers oblong, 0.5–1 mm. long, ca. 0.25 mm. broad, the filaments 0.25–1 mm. long, somewhat inflated, glabrous; disc of minute free lobes, glabrous; ovary ellipsoid, 1–2.5 mm. long, densely sericeous, the style of varying length, filiform, glabrous, the stigma subcapitate, included to exserted (see discussion); pedicel 3–6.5 mm. long. Only a single fruit per inflorescence developing; calyx tube transversely ruptured but persistent as a short ruffle at the base of the drupe; drupe ovoid to almost ellipsoid, 10–18 mm. long, 6–8 mm. in diameter, puberulent at least at the apex; pedicel thickening in fruit.

The proper taxonomic treatment of this species and the preceding, *Enkleia malaccensis*, is somewhat perplexing but it has been my decision to recognize two species, one with two subspecies. There is little doubt that these taxa are derived from common ancestral stock as indicated by morphological similarities and present day distribution. Each of the taxa is allopatric and the possibility of interbreeding between them seems remote because of distance alone.

Enkleia malaccensis is most certainly distinct from *E. siamensis* ssp. *siamensis* as can be demonstrated with any number of morphological or anatomical characters, many of which are apparent to the unaided eye. It is with the introduction of specimens from the Andaman Islands (originally described as *Linostoma andamanica* and here treated as *E. siamensis* ssp. *andamanica*) that difficulties begin. Unfortunately, only two collections from the Andamans are available, and this seriously impairs knowledge of the variability of these plants; but even with these few it is possible to see that they combine characteristics of *E. malaccensis* and *E. siamensis* ssp. *siamensis*. Further, they entirely lack distinguishing characters of their own; otherwise I would recognize three species. Of the characters which are combined, the great majority are from *E. siamensis* ssp. *siamensis*. It is not surprising to find the Andaman plants most closely related geographically with those of ssp. *siamensis*. Char-

acteristics of *E. malaccensis* which are found in ssp. *andamanica* are habit, enlargement of the fruiting peduncle, bract size, and the presence in the leaf of some fibers which are not associated with the vasculature. Some of the more important features which are shared with ssp. *siamensis* are the large number of primary lateral veins, the degree of clefting of the petals, the calyx tube pubescence, the free disc, the mode of fruit development, and the absence of subepidermal fibers.

The Andaman Island plants may have arisen at a time when the morphological characteristics which now delimit the species were still in a state of flux and not yet geographically segregated, or they may be the result of considerable convergent evolution. The former case seems most probable because of the lack of distinguishing characters not represented in other taxa. Whether *E. malaccensis* or *E. siamensis* is primitive or advanced, generalized or specialized, cannot be determined, for both have elements which I consider primitive and advanced.

KEY TO THE SUBSPECIES

a. Leaves densely to sparsely tomentulose, often glabrescent, the submarginal vein well developed; primary peduncle to 5 cm. long; bracts at anthesis borne near the middle of the primary peduncle or below, 2–4(–5) cm. long, 1–1.5 cm. broad; calyx tube 6–8 mm. long; antisepalous stamens subexserted. ..... 3a. *E. siamensis* ssp. *siamensis*.

a. Leaves glabrous, the submarginal vein poorly developed; primary peduncle to 9 cm. long; bracts at anthesis borne above the middle of the primary peduncle, 4–8 cm. long, 1.5–2.5 cm. broad; calyx tube about 5 mm. long; antisepalous stamens included. ..... 3b. *E. siamensis* ssp. *andamanica*.

3a. Enkleia siamensis ssp. siamensis

Linostoma siamense Kurz, Jour. As. Soc. Bengal **39**(2): 82. 1870 (TYPE: *Teysmann 5986*!).

Linostoma scandens var. *cambodianum* Lecomte, Not. Syst. Paris **3**: 127. 1915, "*cambodiana*" (TYPE: *Pierre 511*!).

DISTRIBUTION. Open deciduous forest or scrub in Burma, Thailand and Cambodia. Collected from 100 to 1200 meters altitude. Flowering in January, although buds apparently forming as early as November; fruiting in January, February and March.

Burma. PEGU: Pegu Yomak, e. and w. slopes, *Kurz 3122* (K). **Thailand.** CHAIYAPHUM: Chaeyapuin [Chaiyaphum], *Kerr 19959* (BM). CHIANGMAI: Lampang Mae Saikham, *Wanadorn 1590* (L). CHONBURI: Kanboerie [Chonburi], *Teysmann 5986* (L-isotype of *Linostoma siamense*), *Kerr 10136* (BM), *10620* (BM). NAKON PHANOM: Nawkawn Panom [Nakhon Phanom], *Kerr 8214A* (BM). PHETBURI: Tung Quang, Petchaburi, *Kerr 20601* (BM). PRACHUP: Kan Kradai, Prachuap, *Put 2305* (BM); Hua Hin, *Kerr 16136* (BM). Nang Rawng (?) *Kerr 8214* (BM). **Cambodia.** In montibus Krewand Prov. Tpong [Thpong], *Pierre 511* bis (A, BM, G, GH, K, P); in prov. Peû Lover (see discussion), *Pierre 511* (isotypes of *Linostoma scandens* var. *cambodianum:* A, BM, F, K, L, P); Stung Treng, *Poilane 14229* (P); without locality, *Jullien s.n.* (P).

In the original description of *Linostoma siamense*, Kurz gave the place of collection as, "Siam, Bookit Kathay near Kanburi." Attempts to locate Bookit Kathay were in vain. Re-examination of the handwritten label on the isotype showed the collector's name and number plus, "Daphnoideae. Boekiet Kethaay, Kanboerie, Siam." Therefore, it appears as though Kurz removed the comma following "Kethaay" and inserted the word "near." Teysmann's account of his travels (1863, p. 201) shows that "Boekiet Kethaay" is not the place of collection but the common name! The place of collection is Kanboerie (= Bang Pla Soi, Chanburi, Cholburi, Chonburi, Jolburi or Kanburi) which Teysmann visited for several days toward the end of March, 1862.

Pierre 511 is a collection consisting of two parts. The first, collected in March, 1870, is the more important as it serves as the basis of Lecomte's *Linostoma scandens* var. *cambodianum*. In the original description of this varietas Lecomte gives the location as "Prov. de Pan Louvea." Examination of the numerous sheets of this collection has added these possibilities: Pen Saver, Peû Saver, Peû Sover and Peû Lover. Unfortunately, I have not been able to locate, to my satisfaction, the place of collection. I have the following possibilities: Kompong Svay (ca. 13° N, 195° E), Prey Lovea (ca. 11° N, 105° E) and Lovea (ca. 13° N, 103° E) and therefore have not plotted this collection on the map. The second portion of *Pierre 511* was collected June, 1870, "in montibus Krewand prov. Tpong." The locality is probably Thpong and I have plotted it so. This portion of the collection has been designated as 511 bis.

The displacement of the reduced leaves borne near the base of the primary peduncles has been discussed previously (Nevling, 1961). These leaves generally are only several millimeters in length, although in *Kerr 16136* they are fully developed, normal leaves. This evidence helps secure the hypothesis that these reduced leaves are homologous with the leaves of the vegetative shoot.

Only a very small number of the specimens of this subspecies which I examined were in flower. The description and measurements of the flower are, of necessity, based on few specimens and further variability should be expected.

The final position of the stigma with respect to the calyx tube orifice is dependent upon the amount of elongation of the style. The mechanics of stylar elongation in *Pimelea* has been discussed by Burrows (1960) and a similar mechanism is suspected in *Linostoma* (Nevling, 1961). It is almost certainly in operation in this species of *Enkleia*. The elongation ceases at the time of pollination or shortly thereafter, and the length of the style thus is determined by the pollination time. In *Wanadorn 1590* two floral dissections by Dr. Ding Hou show one with a very short style and the other with an extremely long style. Other collections which I have observed have the style of varying length. Unfortunately, the length of style has been used as a key character to separate *Enkleia* from *Linostoma*, and now the character appears to be useless.

3b. **Enkleia siamensis** ssp. **andamanica** (Hutchinson ex C. E. Parkinson) Nevling, comb. & stat. nov.

Linostoma andamanicum Hutchinson ex C. E. Parkinson, Fl. Andaman Is. 229. 1923, "*andamanica*" (TYPE: *Parkinson 384*!).

According to Parkinson, the plants are found on Baratang and Havelock islands. They are dispersed but very uncommon. They flower and fruit during the hot season. The habit is described by Parkinson as "a woody climber as thick as a man's arm and climbing over the tallest trees, stems hooked."

Andaman Islands. Ali Masfid Reserve, *Parkinson 384* (DD-holotype of *Linostoma andamanicum*, K); without locality, *Parkinson 309* (DD).

See discussion following specific description above.

4. **Enkleia thorelii** (Lecomte) Nevling, comb. nov.

Linostoma thorelii Lecomte, Not. Syst. Paris 3: 127. 1915 (TYPE: *Thorel 2823*!).

Erect shrubs to 0.5 m. tall; young stems terete, strigose and glabrescent, becoming reddish brown, the axillary branches normal. Leaves subopposite to alternate; leaf blades elliptic, 2.5–4.5 cm. long, 1–2 cm. broad, obtuse and mucronate at the apex, cuneate at the base, coriaceous, glabrous, the costa plane above, slightly elevated beneath, the primary lateral veins inconspicuous, ca. 15–20 pairs, the submarginal vein coinciding with the margin, conspicuously thickened; petiole nearly terete, glabrous, 1–3 mm. long. Inflorescences borne from the young shoots, generally simple; each inflorescence 6–12-flowered, subracemiform, the primary peduncle 2–4 cm. long, elongating to 6.5 cm., with most of the elongation above the insertion of the bracts, bearing the reduced leaf of the subtending node near the base, the rachis 1–7 mm. long, the secondary peduncles 1–2 mm. long, the bracts at anthesis opposite to subopposite, borne below the middle of the primary peduncle, keeled to plane, 5–25 mm. long, to 20 mm. broad, minutely strigose, the bracteole borne at the summit of the primary peduncle, linear, to 5 mm. long, minutely strigose, persistent. Calyx tube tubular, 6–11 mm. long, ca. 1.5 mm. in diameter at the orifice, minutely strigose to hirsute without, glabrous within; calyx lobes oblong, ca. 3.5 mm. long, 1.5 mm. broad, spreading, minutely puberulent within; petals cleft to the base, the lobes liguliform, ca. 4.5 mm. long, greatly exserted, erect to spreading, glabrous; stamens inserted in two whorls, the antisepalous ones inserted about 1 anther-length below the petals, subexserted, the alternisepalous whorl inserted about 3 anther-lengths below the antisepalous whorl, included, the anthers oblong, ca. 1 mm. long, 0.5 mm. broad, the filaments thick, 0.25–0.5 mm. long, glabrous; disc of many minute lobes; ovary fusiform, ca. 2 mm. long, very sparsely sericeous, the style filiform, ca. 1 mm. long, glabrous, the stigma clavate; pedicel 2–3 mm. long. Fruit unknown.

DISTRIBUTION. The Kerr specimen was collected in open scrub at an altitude of about 200 meters, flowering in January. Thus far known only from Thailand.

Thailand. NAKON RATCHASIMA: Dun Kuntot, Korat, *Kerr 19930* (BM). UBON: Kemarath [Khemmarat], *Thorel 2823* (P-holotype).

This species is notable for its erect habit, small leaves and large flowers with sparsely sericeous ovary. It is unfortunate that it is so poorly represented in our herbaria.

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THE FLORAL MORPHOLOGY AND RELATIONSHIPS OF KINGDONIA UNIFLORA

ADRIANCE S. FOSTER

THE BROAD COMPARATIVE STUDIES of Bailey (1) and his associates have revealed many examples of the combination of primitive and advanced levels of specialization in the vegetative and reproductive structures of woody members of the Ranales. Indeed, certain ranalian genera are the only known dicotyledons which exhibit such primitive characters as monocolpate pollen, vesselless xylem, and "open," styleless, conduplicate carpels. Despite the significant advances in our understanding of the trends of evolutionary specialization in the xylem and in floral organs, the nature of the truly primitive leaf type in angiosperms remains an unsolved problem. The predominance in the woody Ranales of simple leaves with pinnate-reticulate venation is regarded by Eames (8, p. 421) as "strong evidence that this is a primitive leaf type in the Angiosperms." Bailey (2), however, takes a more conservative or skeptical viewpoint and states that the modern angiospermic leaf may have arisen "from one of several diversified forms of potentially ancestral appendages." In full accord with this cautious approach to the problem, I have already raised the question of whether the "closed" reticulate type of venation, so characteristic of living angiosperms, may not have evolved from open dichotomous vasculature (9). This possibility is clearly indicated by the remarkable dichotomously veined leaf of *Kingdonia uniflora*, an herbaceous perennial which is classified at present as a member of the Ranunculaceae (10, 11, 12).

The occurrence of dichotomous foliar venation in a plant of presumed ranalian affinities deserves full consideration in any theory of foliar evolution and emphasizes the need for a comprehensive study of *all* aspects of structure and morphology in *Kingdonia*. For this reason an investigation of the morphology and vasculature of the floral organs of this genus has been undertaken and the results are presented in this paper.

MATERIALS AND METHODS

The flowering specimens used in my study were secured, through the kindness of Professor Yu-Wen Tsui, from the following Shensi collections of *Kingdonia* deposited in the herbarium of the Northwestern Institute of Biology at Wukung, Shensi Province, China, viz.: *Liu & Chun 1307*, collected September 28, 1937, on Taipaishan; *Ho, s.n.*, Taipaishan, Fan Yang Szu (Pasturing Sheep Temple); and *Fu 12296*, collected June 7, 1959, on Taipaishan. Grateful acknowledgment is made to Dr. Shiu-ying

Hu, of the Arnold Arboretum, Harvard University, for translating into English the Chinese data included with the Ho collection of *Kingdonia*.

Despite the fragile and desiccated condition of the material, the combined use of cleared specimens and serial microtomed sections made it possible to study many features of floral morphology in considerable detail. All flower buds and flowers were first cleared in 2.5% NaOH and, after thorough washing in water, transferred to cold concentrated chloral hydrate. Specimens cleared in this way proved suitable for drawings of the general organography of the flower and were subsequently dehydrated and lightly stained with safranin. After staining, the individual organs of some of the flowers were dissected from the receptacle and mounted directly in "Piccolyte." Other flowers, as well as the buds, were dehydrated by the tertiary butyl alcohol method, infiltrated with "Histowax," sectioned 7–8μ in thickness, and stained with a combination of safranin and light green.

I wish to thank Mr. Roy L. Taylor for his skillful assistance in all phases of the embedding, sectioning, and staining of the floral material. I am also greatly indebted to my wife who prepared the drawings reproduced in this paper as FIGS. 2–7, assembled the photomicrographs and assisted me in proofreading the manuscript. Thanks are also due Mr. Victor Duran for his skill and patience in making the photomicrographs.

GENERAL ORGANOGRAPHY OF THE FLOWER

According to Balfour and Smith's (5) description of the type material collected by F. Kingdon Ward in northwestern Yunnan Province, China, the solitary, apetalous flower of *Kingdonia* is borne on a naked scape 7–10 cm. long and consists of 5 sepals, 10–15 stamens, and 5–7 carpels. My observations, restricted to a study of flowering specimens from a montane area in Shensi Province, differ in several important respects from this description.

In the first place, it seems more appropriate to designate the spirally arranged perianth members as "tepals" rather than as "sepals" (FIG. 1). The latter term implies the former existence of petals in the flower of *Kingdonia*, but no evidence of vestigial petals or their traces was found in either cleared or sectioned flowers. Furthermore, it is obvious even from the limited material examined that the number of perianth members is inconstant. In some flowers five tepals are present (FIG. 1), but flowers with six or seven tepals have also been observed. These fluctuations clearly suggest that a well-defined "calyx," in the formal sense, is not present.

A more serious divergence between Balfour and Smith's description and the present study concerns the nature of the androecium. In all the flowers I have examined, the androecium consists of an outer series of 8–12 spirally arranged staminodia and a more centrally located series of 3–6 stamens, each of which is demarcated into anther and filament (FIGS.

1, 8, 10, 11). Although no organs morphologically intermediate in character between staminodia and stamens were observed, the study of a wide range of flowers might reveal such transitions. Whether the larger number of stamens (10–15) cited in Balfour and Smith's description represents a condition peculiar to the material from Yunnan or whether they failed to discriminate between staminodia and stamens must remain open questions for the present.

FIG. 1. Organography of a mature flower with five tepals, numerous staminodia, six stamens, and seven carpels, × 14. (Drawn from a cleared specimen, *Fu 12296*, by Mrs. Emily R. Reid.)

The apocarpous gynoecium of the flower of *Kingdonia* is composed of 5–8 spirally arranged carpels (FIGS. 1, 2, 18). Following pollination, the tepals, staminodia, and stamens fall from the receptacle, and the stylar portion of each of the enlarging carpels gradually becomes bent or recurved over the dorsal edge of the ovary (FIGS. 2, 21–24). This beaked character of the developing carpel and fruit is highly distinctive of *Kingdonia* and was noted in the brief descriptions of Balfour and Smith (5), Diels (7), and Wang (15).

COMPARATIVE MORPHOLOGY OF FLORAL ORGANS

One of the interesting results of the present study was the discovery of the general similarity in the nodal anatomy of *all* the appendages of the flower. The vascular system of most of the receptacle is a typical eustele in which, as the result of interfascicular cambial activity, a single well-defined gap is associated with the divergence of the vascular supply of each of the tepals, staminodia, stamens, and lower carpels. In contrast, the vasculature of the upper portion of the receptacle consists entirely of the traces of the inner carpels, and no "residual" xylem or phloem strands appear to exist (FIG. 18).

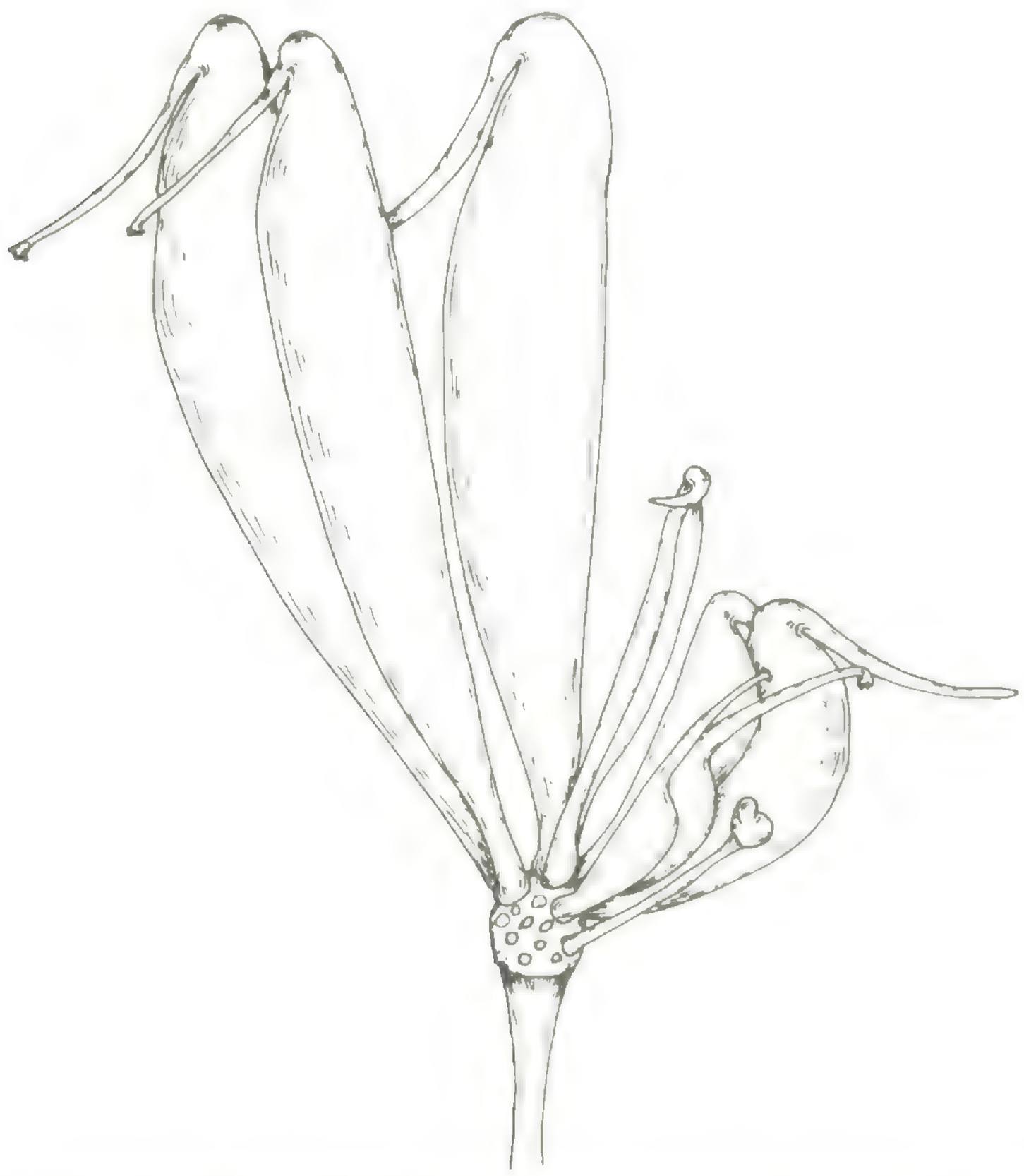

FIG. 2. Form and spiral arrangement of a series of eight carpels of *Kingdonia* (*Ho, s.n.*) at various stages of enlargement, × 8. Except for a single persistent staminodium (at lower right) all other floral organs have fallen from the prominent receptacle. Note dorsally reflexed styles of three largest carpels at the left.

The following description and interpretation of the form, general structure, and venation of the floral organs of *Kingdonia* is based largely upon the examination of mature flowers. Although much care was devoted to restoring the structure of flower buds, the results in some respects were quite disappointing. As a consequence, many important aspects of floral

morphology, such as the early differentiation of the anther and the structure and vasculature of the ovule, cannot be described until adequate fixed material of all stages in floral development becomes available.

Tepals. A comparison of the cleared and stained tepals revealed interesting variations in both form and venation (FIGS. 3–7). Only a single example of a lobed tepal was observed in the present study (FIG. 6). The lamina of this remarkable appendage terminates in two short lobes separated by a deep and clearly defined sinus. Whether or not this form of tepal should be regarded as a rare "anomaly" can, of course, only be determined by a survey of many flowers. It is entirely possible that three- or even five-lobed tepals may occasionally develop. Most commonly, and in agreement with Balfour and Smith's description of the "sepals," the tepal of *Kingdonia* is a simple foliar structure consisting of a short petiole and an elliptical-oval, prominently acuminate lamina (FIGS. 3–5).

Before describing the venation pattern of the tepals, it is essential to comment briefly on the structure of the tepal traces near their point of divergence from the eustele of the receptacle. A study of thin serial transections of one of the flowers showed that each trace consists of two more or less discrete strands of primary xylem which appear to be independently connected with the receptacle bundles bordering the single gap. However, the limitations of the material prevented a fully satisfactory reconstruction of the exact nature of the subnodal connections and origin of the tepal traces.

The basal portion of each tepal is traversed by the unbranched extension of its double trace, which, in cleared specimens, usually consists of two separate but closely spaced strands of xylem. In the lower region of the tepal lamina, this double bundle gives rise to a midvein and two lateral veins, one or both of which may branch dichotomously (FIGS. 4a–6). No evidence of anastomoses or commissural veinlets was found, and hence the tepal venation in *Kingdonia* is simple and "open" in type. However, the exact mode of origin of the midvein and the two main lateral veins from the double bundle fluctuates even among the tepals of one perianth and may be conveniently described under the two following "types."

TYPE 1. In this very common type, the midvein and one of the lateral veins of the tepal lamina represent respectively the central and outer branches of one of the main xylem strands of the double trace (FIGS. 3, 5, 6). However, the level at which divergence and dichotomy of the main strands of the trace occur varies considerably. In many tepals, the single dichotomy which yields the midvein is near or at the level of divergence of both of the lateral veins. But FIG. 3 shows that the dichotomy may take place well above the point of divergence of the other main lateral vein.

TYPE 2. The distinctive feature of this less common type is the dichotomous branching, at approximately the same level, of *each* of the two xylem strands of the double bundle and the union of the central strands

to form the midvein of the tepal (FIG. 4a–b). The two outer strands resulting from these dichotomies constitute the main diverging lateral veins of the lamina. A detailed study, with the aid of dark field illumination, showed that the two central strands which join to form the midvein are relatively slender and often unequal in size (FIGS. 4b, 7).

As FIGS. 3–6 clearly indicate, there is no apparent correlation between these two types of midvein origin and the degree of branching of the main lateral veins. Type 1 may be associated with tepals in which both lateral veins remain unbranched and terminate blindly in the upper half of the lamina, or one or both of the laterals may dichotomize. In the latter case, the *inner branch* very commonly is longer and more highly developed than its sister branch. A striking example of this is shown in the bilobate tepal in which the lateral lobe is vascularized by the stronger inner branch of one of the lateral veins (FIG. 6).

A few comments are appropriate regarding the interesting variations in the amount of xylem differentiated at various levels in the midvein. Near its point of origin, the midvein is relatively slender and comparable in this respect to the main lateral veins. Quite commonly, however, the upper portion of the midvein is conspicuously thicker as the result of the increase in number of tracheary elements. At its point of termination in the apex of the tepal, the midvein is usually dilated, suggesting the possibility that it is associated with a hydathode.

Staminodia and Stamens. As mentioned earlier, the outer members of the androecium are clearly defined staminodia (FIG. 1). Each staminodium consists of an elongated filamentous stalk which terminates abruptly in an apically dilated "knob." The vasculature is represented by a single unbranched vein which extends vertically through the stalk and then curves adaxially into the dilated end of the staminodium (FIG. 8). Although serial transections revealed no traces of rudimentary or abortive microsporangia, the dilated portion of the staminodium is quite comparable in general form and venation with the corresponding sterile region of the anther (compare FIGS. 8 and 11). On the other hand, a definitive character of the staminodial apex is the presence on its adaxial side of a median groove or furrow. As seen in transectional view, the epidermal cells which line the groove occur directly over a tissue comprised of cells which are much smaller and more deeply stained than the bulk of the parenchyma cells of the staminodium (FIG. 9). On the basis of this histological evidence, the groove may be glandular or "nectariferous" and may secrete substances which attract insect visitors to the flowers.

Each of the stamens, like the staminodia, is vascularized by a single unbranched bundle which diverges at the juncture of anther and filament into the broad area of sterile tissue separating the two pairs of microsporangia (FIGS. 10, 11). Although the sporangia are protuberant and superficially may appear "terminal," their position with reference to the anther as a whole and to the plane of dehiscence is more accurately described as "latrorse-extrorse." This is shown by FIGS. 10, 11 which re-

spectively depict abaxial and adaxial views of mature, cleared stamens, and illustrate the oblique, more or less abaxial (i.e., extrorse) line of dehiscence between the members of each pair of sporangia.

The tissues of the young stamens of the flower buds which were sectioned were so badly collapsed and distorted that the following description and interpretation of the structure of the microsporangia is necessarily based on the study of mature, dehiscent anthers. FIGURE 12 represents a transection of an anther at the time of dehiscence and shows the remains of the partitions which separated the members of each pair of sporangia. The confluent "pollen sacs" contain "normal" pollen grains (see also FIGS. 13–16), small tetrads, and apparently many examples of shrunken abortive cells. At this late stage in maturation it is impossible to describe with any accuracy the cellular structure of the sporangium walls. The dark "lining" of the pollen sacs may correspond to the remains of the tapetum and middle layers of the wall but there is no certainty on this point. In contrast, the endothecium or "fibrous layer" is well preserved and consists of two sharply delimited semicircular layers of cells with bandlike thickenings which jacket the protuberant portions of the confluent sporangia. These strips of endothecium are not continuous across the sterile portion of the anther, nor have cells with similar structure been observed bordering the internal edges of the sporangial cavities.

The taxonomic and phylogenetic interest of information on pollen morphology in *Kingdonia* is emphasized by the present classification of this genus in the Ranunculaceae, a family characterized, according to Bailey and Nast (3), by tricolpate or derived forms of pollen. Because of my extremely limited material, a somewhat "unconventional" technique was employed in securing permanent whole mounts of pollen grains. Following the usual clearing in NaOH and chloral hydrate, the stamens were dehydrated, stained in dilute safranin and the mature anthers "squashed" directly in the "Piccolyte" before adding the cover-glass. Selected examples of pollen processed in this way are shown in FIGS. 13–16.

A comparison of polar and side views clearly indicates that the pollen grain is provided with three longitudinal furrows or colpi (FIGS. 13, 15, 16). Although it has not been possible to study germinating pollen, there is some suggestion that a definable pore or aperture is located in each of the colpi. In the grain shown in median optical view in FIG. 13 the delicate "intine" appears to have evaginated as a short tubular process from the center of each of the furrows. On this basis it would appear justifiable to classify the pollen of *Kingdonia* as tricolporate in type. The exine of mature grains is moderately thick and when seen in surface view exhibits a complex foveate-reticulate structural pattern (FIG. 14).

Carpels. Although the general form and uniovulate nature of the carpels of *Kingdonia* have been described by Balfour and Smith (5) and Diels (7), their accounts are very brief and include no information on early ontogeny or vasculature of these organs. On the basis of the present investigation it is believed that a relatively full description may now be

given of some of the early and critical stages of development and vascularization of the carpel. The most serious gaps in my description and interpretation concern the ontogeny and vasculature of the single pendulous ovule developed in each carpel (FIG. 20). Despite the greatest possible care, the tissues of the ovule appeared collapsed and disorganized at all stages, and the problem can only be solved by the use of adequately fixed and preserved material (see also FIG. 19c).

Before presenting the details of carpel ontogeny it is necessary to describe briefly the general pattern of growth which leads to the adult form of the carpels. At anthesis, the carpel consists of a very short basal stipe, a laterally flattened ovary, and an erect or slightly recurved style with a terminal papillate stigma (FIGS. 1, 21). When the carpels are approximately 2–3 mm. in total length, they contain a single ovule attached to the ventral side of the carpel wall (Fig. 20). As growth continues, the basal stipe elongates, the ovarian region increases conspicuously in length and width and the style becomes reflexed over the upper dorsal edge of the carpel (FIGS. 21–24). According to Wang (15), the mature fruit of *Kingdonia* is a one-seeded achene and exclusive of the recurved "beak" is 8 mm. long and 2.2 mm. wide. A carpel of approximately similar dimensions is shown in FIG. 24.

A transection of the central region of a developing flower bud showing three young carpel primordia is depicted in FIG. 17. At this early stage, the primordia are 200–275 μ in height and throughout most of their length are prominently conduplicate structures. However, because of their spiral arrangement on the receptacle these primordia are not cut at the same level, and the lower primordium in FIG. 17 is represented by a section through the short basal stipe. Comparison of serial sections indicates that the post-genital fusion of the carpel margins to form the closed locule occurs in an acropetal direction. The carpel primordium at the upper right in FIG. 17 shows an early stage in the fusion of the margins, while the primordium at the left has been sectioned at a slightly higher level and exhibits an open conduplicate structure. In both of these carpels a single ovule primordium has arisen distal to the margin of the carpel. Thus the placentation in *Kingdonia* is obviously submarginal in type.

The continued differentiation and enlargement of the carpel is accompanied by the progressive acropetal fusion of the carpel margins and the development of a simple but highly distinctive type of vasculature. A relatively advanced stage in the closure of the carpel is shown in FIGS. 19a–e which represent transections cut at successively higher levels through a carpel approximately 1 mm. in height. Although complete union between the margins and outer adaxial surfaces of the carpel wings has produced a closed locule in the lower portion of the ovary (FIG. 19b, c), the upper third of the carpel, including the style is still unsealed and conduplicate in organization (FIG. 19e). Limitations of material prevented a study of the later and final phases of closure of the carpel, and serial transections of a carpel 6.75 mm. in height showed no evidence, except in the lower adaxial portion of the style, of conduplicate structure.

Each of the spirally arranged carpels of *Kingdonia* is vascularized by a single trace which, in young carpels, consists of a strand of xylem flanked and partially enclosed by two well-defined strands of phloem (FIG. 18). Soon after its extension into the basal region of a carpel, the trace divides tangentially into a dorsal (abaxial) and a ventral (adaxial) bundle. This aspect of carpellary vasculature is shown in the bases of three of the outer carpels in FIG. 18 and is further illustrated in the photographs of the cleared carpels represented by FIGS. 22–24. The structure and course of the dorsal and ventral bundles in a young, apically conduplicate carpel are shown in the transectional views depicted by FIG. 19a–e. The relatively weak development of xylem in the ventral bundle is evident even in sections of the stipe (FIG. 19a). At successively higher levels the ventral bundle appears to consist wholly of phloem, and the strand terminates its development near the point where the carpellary margins are still open and conduplicate (FIG. 19d). In contrast, the dorsal bundle is more robust, and the existence of both phloem and xylem is evident at high levels in the carpel (FIG. 19e). During the further enlargement of the carpel, the dorsal bundle continues its more rapid development and ultimately extends without branching into the lower region of the style. FIGURES 21–24 clearly suggest that xylem development in the dorsal bundle is precocious, acropetal, and continuous, in contrast to the discontinuous and bidirectional pattern of early xylem formation within the ventral bundle.

During the late phases of closure of the upper part of the carpel, the ventral bundle dichotomizes into two slender branches which terminate blindly near the top of the ovary but do not extend into the base of the style (FIG. 24). The point at which the bifurcation of the ventral bundle occurs appears to be below or in the immediate vicinity of the attachment of the ovule to the placenta. The ventral bundle shown in FIG. 19b, for example, although devoid of xylem, appears somewhat "double" in structure. Transections of carpels 6–7 mm. long show that each of the branches of the ventral bundle consists of well-defined phloem and xylem. Unfortunately, however, the ovule in each of these carpels appears abortive and collapsed, and there was no convincing evidence of the derivation of an ovule trace from either of the ventral strands.

A few observations were made of the structure and vasculature of apparently mature fruits. No evidence of *any* venation was seen in the carpel "walls" and it seems clear that the type of vasculature represented in FIG. 24 is typical of both the carpel and the mature achene of *Kingdonia*. During the development of the carpel into a fruit, the dorsal and ventral veins become more or less completely jacketed by sclerenchyma, and the surface cells which line the locule develop remarkable reticulate bands of secondary wall thickening. The prominent beak of the achene is likewise composed largely of sclerenchyma, the initiation of which occurs in the upper region of the styles of comparatively young carpels and proceeds basipetally into the upper portion of the ovary.

DISCUSSION

In the light of current phylogenetic interpretation of floral organs in both woody and herbaceous ranalian plants, the flower of *Kingdonia* appears to show a combination of primitive and advanced levels of specialization. For example, the marked fluctuation in the number of tepals, staminodia, stamens, and carpels, their spiral arrangement on the receptacle, and the absence of fusion between any of these organs point to a rather primitive level of floral organization. On the other hand, the form and vasculature of the stamens and carpels seem decidedly advanced as compared with the foliaceous reproductive structures in the flowers of such woody genera as *Degeneria*, *Austrobaileya*, and *Himantandra*. The following discussion attempts to summarize the anatomical evidence secured by the present study and to evaluate it with particular reference to (a) the phylogenetic significance of the remarkable dichotomously veined leaf of *Kingdonia* and (b) the problem of the systematic affinities of this genus.

The tepals, despite their small size and typically simple form, are the only floral organs in which the vasculature offers points for *direct* comparison with the foliage leaf (FIGS. 3–7). The nodal anatomy of the tepal is unilacunar, as in the leaf, and the double trace seems to represent merely a simplification of the system of four traces which vascularizes the foliage leaf. Indirect evidence in support of this interpretation is provided by the cataphylls of *Kingdonia*. These scale leaves occasionally develop a rudimentary lamina, and in such cases they are vascularized by two well-defined traces. Further indication of the fundamental resemblance between the vasculature of tepal and leaf is shown by one of the modes of origin of the tepal midvein. As illustrated in FIGS. 4 and 7, this unbranched vein may arise from the union of the two central branches formed by the dichotomy of each of the tepal traces. A similar transition from an even to an odd number of main veins occurs in the base of the median lamina segment of the foliage leaf but results in this case in the formation of three systems of dichotomizing veins (cf. Foster and Arnott 11, *Figs. 5, 7*). In connection with these comparisons it is interesting to note the marked resemblance between tepal vasculature in *Kingdonia* and certain forms of cotyledonary venation in the angiosperms recently discussed by Bailey (2). The distinctly asymmetrical derivation of the tepal midvein shown in FIG. 3 is matched in certain types of cotyledons which develop an odd number of veins and the venation pattern represented in FIG. 4a, b corresponds very closely to another widespread type of cotyledonary vasculature (cf. Bailey 2, *Figs. 2 E, F*).

Bailey's (2) comprehensive surveys of the nodal anatomy of cotyledons, foliage leaves, and floral organs provide excellent evidence that the two-trace unilacunar node represents the primitive condition in angiosperms. On the basis of this interpretation, the probable nature of the *complete* vasculature of the primitive leaf type in angiosperms requires careful consideration. Bailey (2) has advanced the suggestion that the "mid-vein

of angiospermic appendages may have evolved by the approximation and fusion of two independent systems of vasculature." This idea implies that the venation of primitive leaves was not "pinnate" in the strict sense of the term but may have resembled certain "pseudo-palmate" or transitional forms of cotyledonary vasculature (Bailey 2, *Fig. 2A, C, G*). In this connection, is it not possible that the leaf of *Kingdonia* — notable for its unilacunar node, its four leaf traces and its palmate system of open dichotomous venation — may typify *one* of the ancient forms of foliar vasculature in the angiosperms? In my opinion, the occurrence of a two-trace and open dichotomous type of vasculature in the tepals of this genus lends additional weight to this theory. Although it may be argued that the persistence of a primitive leaf type is improbable in an herbaceous plant, the family Nymphaeaceae appears to have retained primitive forms of stamens (14), and vessel members with scalariform perforations occur in the xylem of *Paeonia* and *Hydrastis* (8). From these examples there seems to be no *a priori* reason to assume that the dichotomous vasculature of *Kingdonia* must be "specialized" or the result of "reversion" merely because this genus is herbaceous, rather than woody, in habit.

In contrast to the double-trace pattern of vasculature of tepals, each of the stamens of *Kingdonia* is vascularized by a single unbranched bundle (Figs. 10, 11). This fact, coupled with the clear demarcation of anther and filament and the latrorse-extrorse dehiscence of the paired sporangia, indicates a comparatively advanced type of stamen. The morphological and phylogenetic significance of the staminodia, which are likewise unifasciculate appendages, is problematical. However, their inconstant number and their position *below* the stamens suggest an evolutionary origin from fertile microsporophylls.

Like the stamen, the carpel of *Kingdonia* also seems relatively specialized in both form and vasculature, especially when compared with the apparently primitive carpel types which occur in such woody ranalian plants as *Drimys piperita* and *Degeneria* (4). In these species the carpel shows no distinction of an ovary, style, or terminal stigma but is a stipitate, unsealed, conduplicate organ bearing numerous ovules on its inner face between the median and lateral veins. The advanced level of specialization of the stipitate carpel of *Kingdonia* is shown by the clear demarcation between ovary, style and stigma, by the development of a single ovule and by the simple and sparse pattern of vasculature (Figs. 20, 24). Although the conduplicate and open structure of the carpel primordia in *Kingdonia* suggests the persistence of a primitive type of ontogeny, the closure of the carpel occurs relatively early and results in a sealed ovary without a definable ventral suture. The mature vasculature consists of an unbranched dorsal and a forked ventral vein, both derived from the single trace which enters the stipe region of the carpel.

As mentioned earlier in this paper, it proved impossible because of technical difficulties, to determine the nature of the "ovule trace" in *Kingdonia*. The bifurcation of the ventral strand occurs near the point of attachment of the ovule to the inner ventral surface of the carpel and

it is probable that the vasculature of the ovule is derived from one or possibly both of these traces. In this connection, the venation of the carpels of certain members of the Ranunculaceae offers certain points for comparison with the situation in *Kingdonia*. According to Chute (6), the carpel of various species of *Anemone*, *Clematis*, and *Hepatica* is vascularized by a single trace which divides into a dorsal and ventral vein. Near the top of the ovarian cavity, the "fused ventrals" divide into three strands; the median represents the ovule trace, and the two laterals continue into the style. In *Kingdonia*, however, the two branches of the ventral bundle terminate near the base of the style which is vascularized exclusively by the unbranched dorsal bundle (FIG. 24).

In conclusion, it seems appropriate to discuss briefly the bearing of the evidence from leaf and flower on the systematic affinities of *Kingdonia*. As I have recently pointed out (10), the original classification of *Kingdonia* in the Ranunculaceae by Balfour and Smith (5) was accepted without question by Diels (7) and Janchen (13), and the same taxonomic assignment of this genus was later adopted by Wang (15) and Hutchinson (12). Admittedly the herbaceous habit, polymerous flowers and one-seeded achenes of *Kingdonia* are duplicated, at least in a superficial way, in such ranunculaceous genera as *Thalictrum* and *Anemone*. But in my opinion, the *totality* of morphological and anatomical evidence derived from my studies on the leaf and flower strongly indicate that *Kingdonia* is a "relict" genus, without obvious affinity to any ranalian family, including the Ranunculaceae. Prominent among the "unique" and isolated features of *Kingdonia* are the dichotomously veined foliage leaf and the two-trace vascular system of the tepals. Comparable types of foliar vasculature do not occur in any of the genera of Ranunculaceae which I have studied or which have been described anatomically in the literature (10). A similar but less decisive "remoteness" is shown by the pollen grains of *Kingdonia* (FIGS. 13–16). These structures appear to be tricolporate in type and when more thoroughly studied and compared with the pollen of other ranalian plants may support the removal of *Kingdonia* from the Ranunculaceae.

Many important morphological aspects of *Kingdonia* remain for future investigation. These include the determination of the chromosome number, the morphology of the tracheary elements, the study of the seedling (with particular reference to cotyledonary vasculature), and information on the development and structure of the embryo sac, endosperm, and embryo. When these gaps in our present knowledge have been bridged, I suspect that *Kingdonia* will ultimately be treated as the representative of an independent and "relict" family within the Ranales.

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EXPLANATION OF PLATES

PLATE I

FIGS. 3–7. FORM AND VENATION PATTERNS OF TEPALS OF *Kingdonia* [*Fu 12296*]. 3. Origin of midvein and lateral vein from dichotomy of one strand of double trace. × 7. 4a. Origin of midvein by union of central branches of both dichotomizing strands. × 6. 4b. Enlargement of region of vein-union represented in 4a. × 30. 5. Tepal showing prominent dichotomous branching of each lateral vein. × 6. 6. Form and vasculature of a bilobed tepal. × 7. 7. A further example of dichotomy of both strands of tepal trace and union of the two short central bundles to form midvein. × 30 — note close approximation of central bundles as compared with 4b. For further explanations, see text.

PLATE II

FIGS. 8–12. STAMENS AND STAMINODIA OF *Kingdonia*. 8. Cleared staminodium [*Ho, s.n.*] showing general form and vasculature. × 32.5. 9. Transection of apical region of staminodium [*Fu 12296*] showing adaxial groove and single vein.

× 135. 10, 11, Cleared stamens [from *Ho*, *s.n.*], showing vasculature and the orientation and plane of dehiscence of the microsporangia, × 32.5; 10, abaxial view; 11, adaxial view. 12, Transection of dehiscent anther, × 135 — note pollen grains and clearly delimited endothecium.

PLATE III

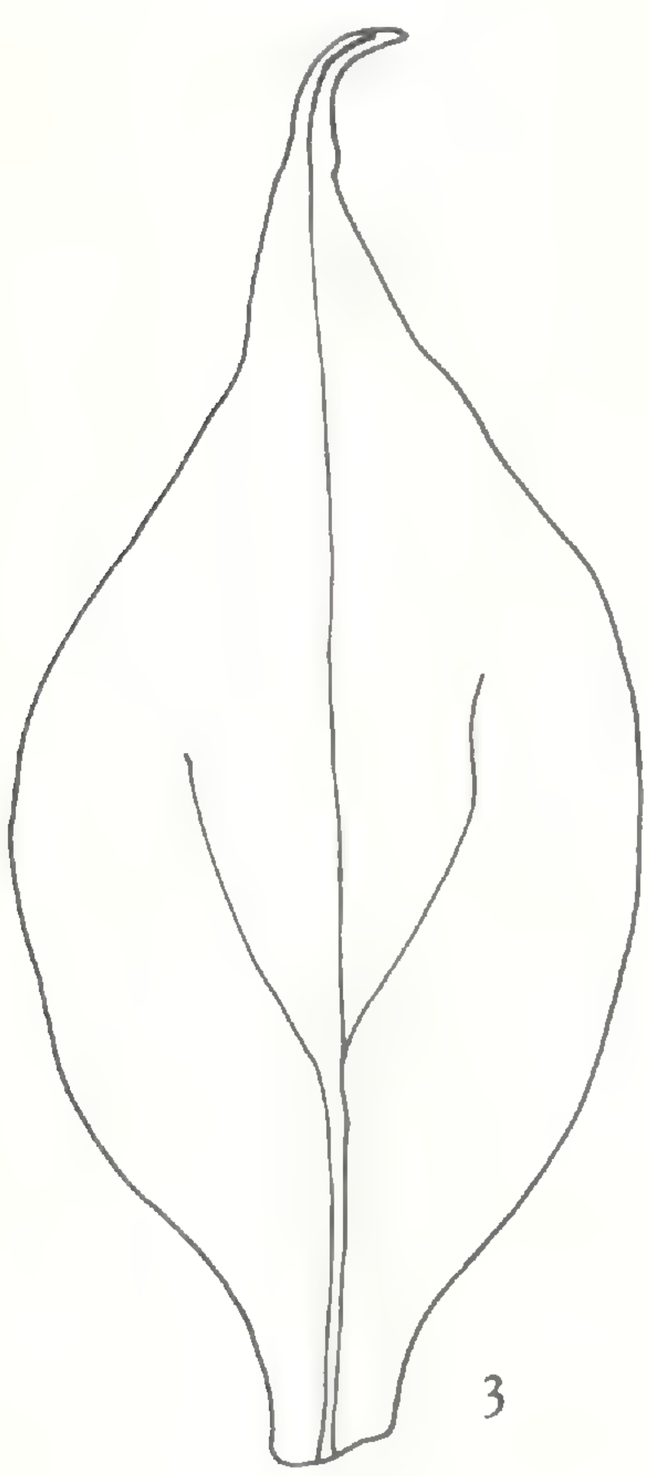
FIGS. 13–17. POLLEN AND CARPELS OF *Kingdonia*. 13–16, Mature pollen grains [from *Fu 12296*], × 1480. 13, Polar view, showing tricolporate structure. 14, Same grain at a higher focal plane, illustrating structural pattern of exine. 15, 16, Side views of pollen grains with longitudinal colpi. 17, Transection of central region of flower bud [*Liu & Chun 1307*] to illustrate young stages of carpel development, × 295. Note conduplicate nature of carpel primordium at left and fused margins of young carpel at upper right.

PLATE IV

FIGS. 18–20. VASCULATURE AND DEVELOPMENT OF CARPELS. 18, Transection of flower [from *Fu 12296*] with seven carpels, the outer five of which are attached to the receptacle, × 138. Note particularly that each of the traces of the two uppermost carpels consists of a single xylem strand flanked by two phloem strands. 19a–e, Transections, at successively higher levels, of one of the carpels shown in Fig. 18, × 138. 20, Longitudinal section of a carpel about 2 mm. high (exclusive of reflexed style) showing the attachment of the single pendulous ovule to the ventral wall [*Ho*, *s.n.*], × 22.

PLATE V

FIGS. 21–24. CLEARED CARPELS, selected from gynoecium [from *Ho*, *s.n.*] shown in Fig. 2 and photographed with dark-field illumination. 21, Carpel, approximately 2 mm. in height, showing ovary, style, and papillate stigma, × 32.5 — note precocious and acropetal development of xylem in dorsal bundle. 22, Older stage than preceding figure, showing dorsal bundle extending into base of reflexed style and an early phase of xylem development in ventral bundle, × 19. 23, Still later stage illustrating apparent bidirectional and interrupted pattern of xylem differentiation in ventral bundle, × 19. 24, Carpel approximately 7.5 mm. high (exclusive of reflexed style) showing complete vasculature, × 19 — note dichotomy of ventral bundle near top of ovary.



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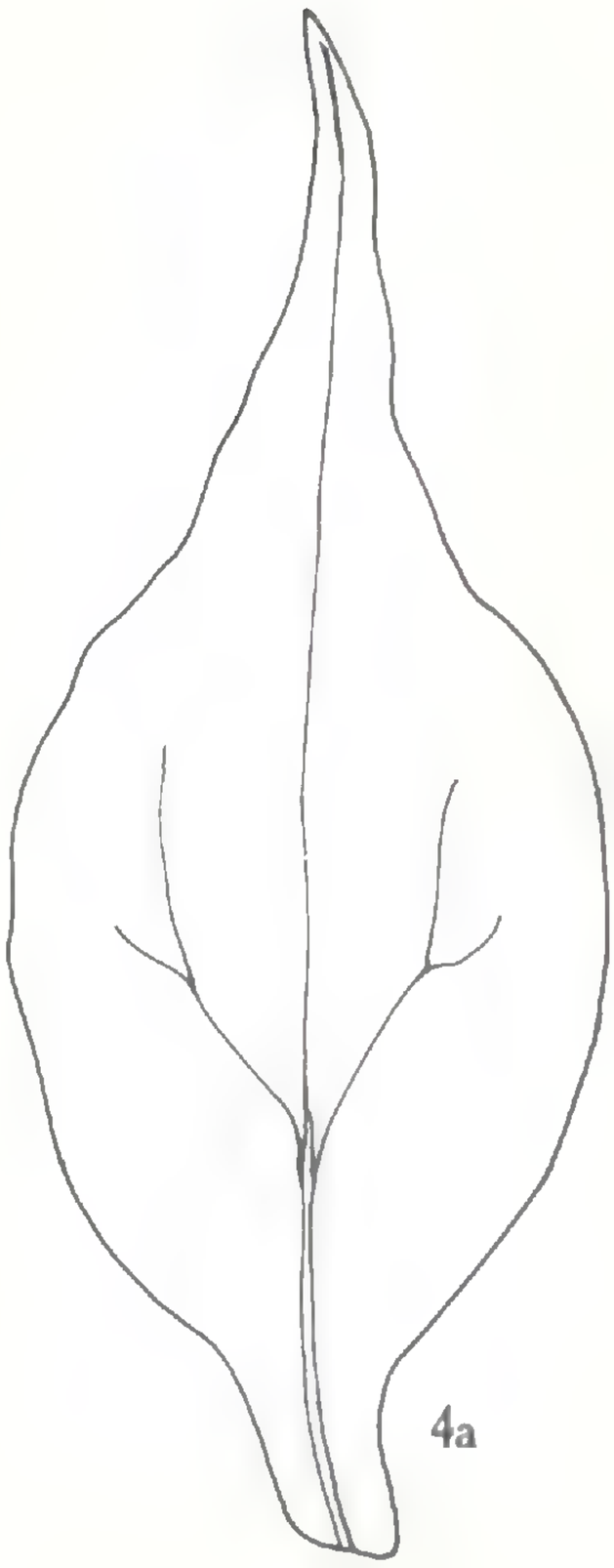

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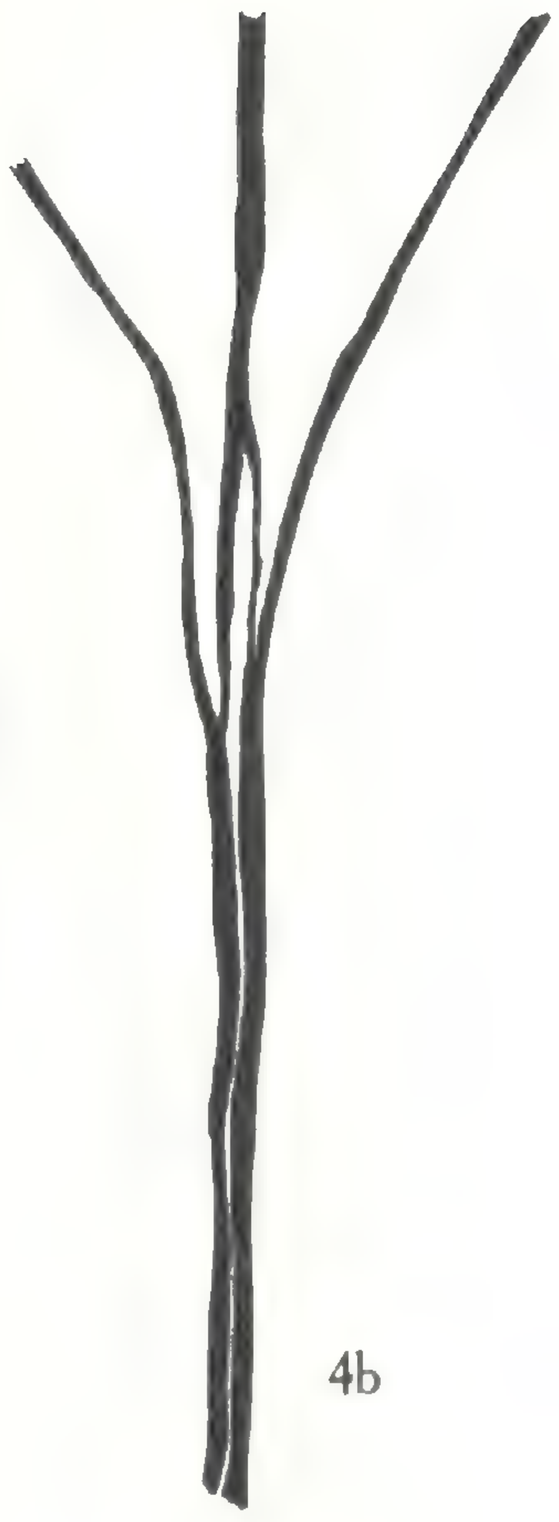

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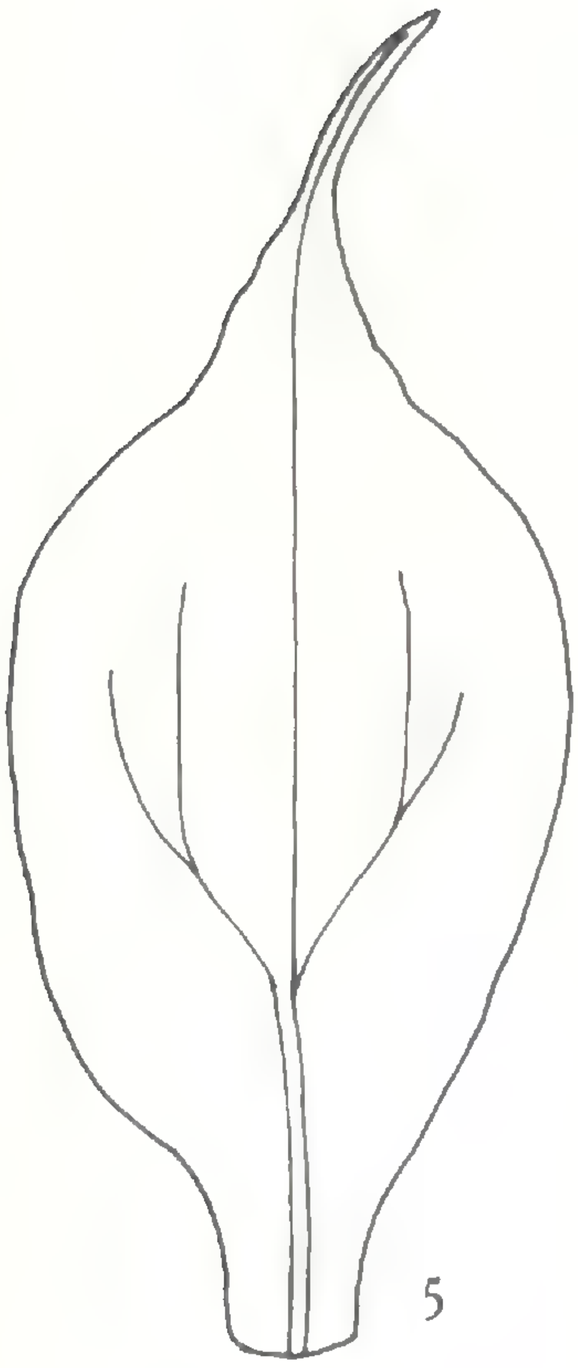

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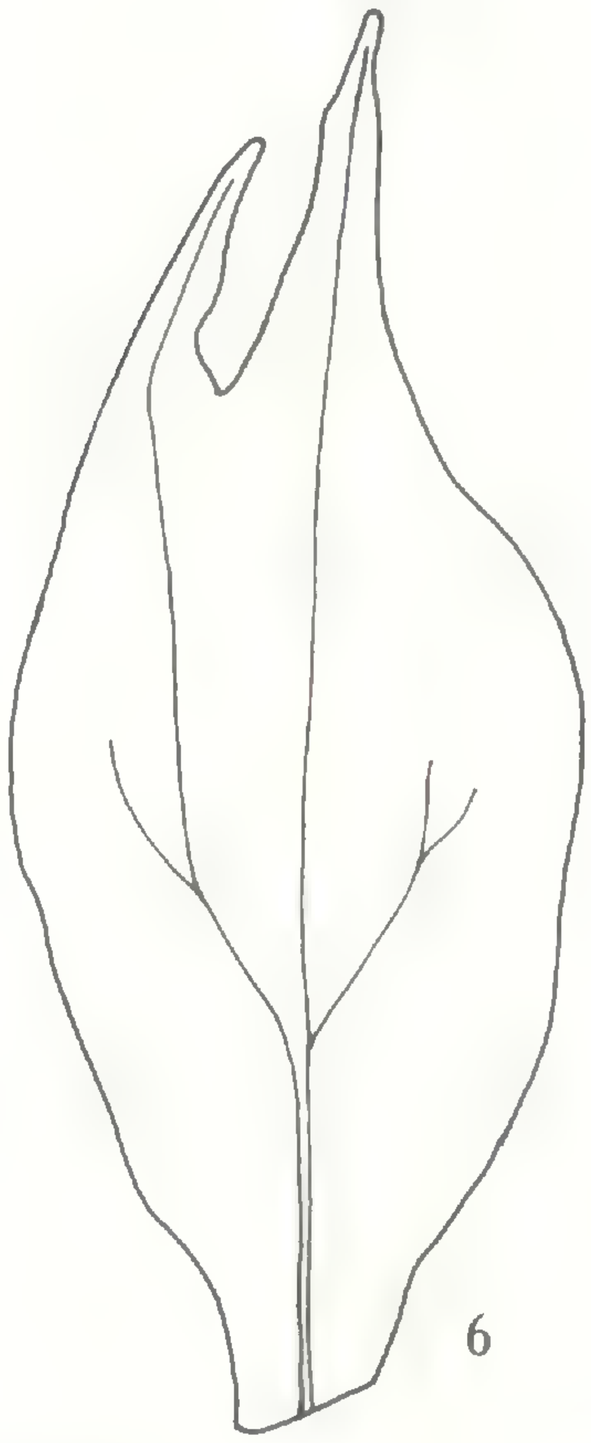

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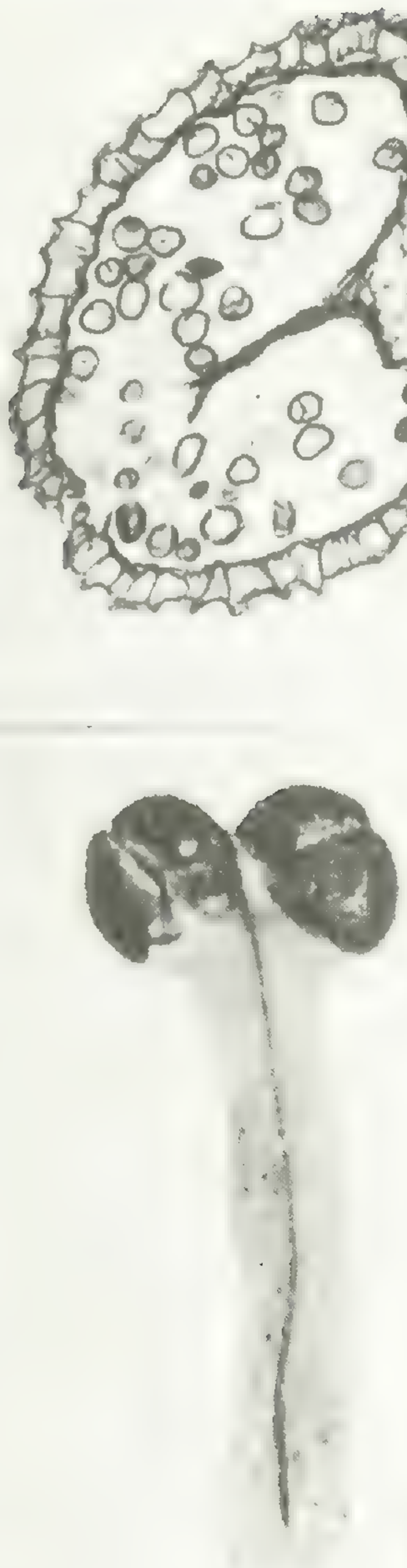

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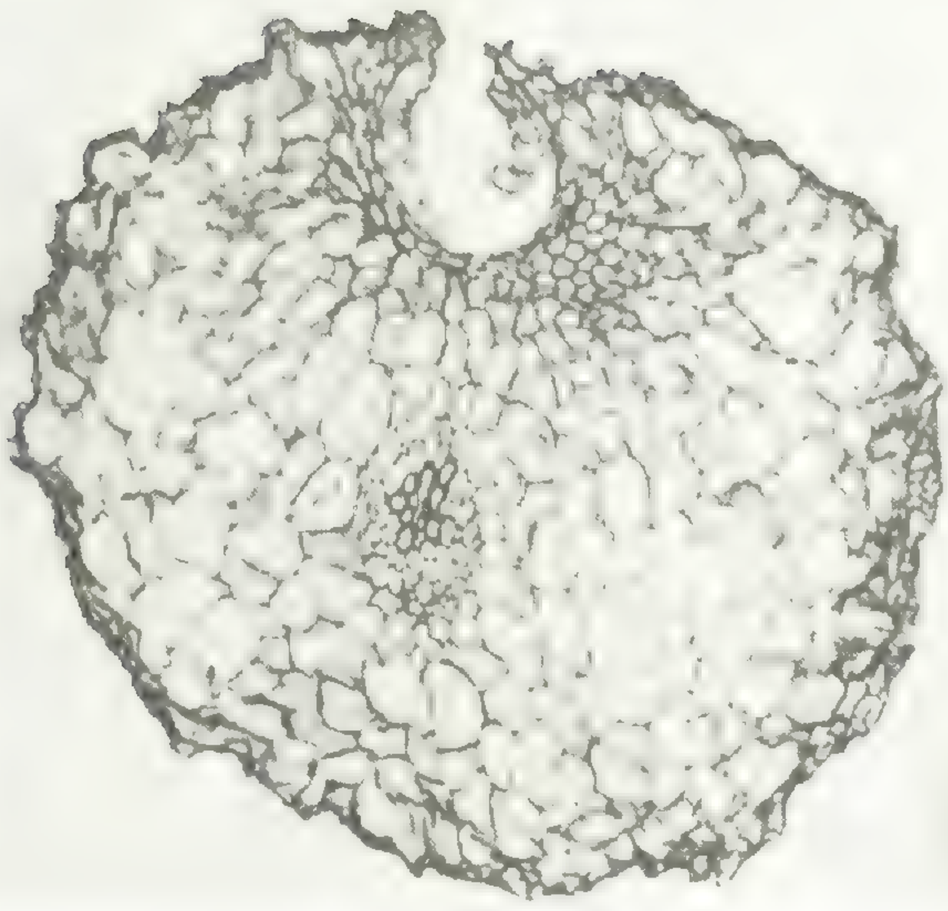

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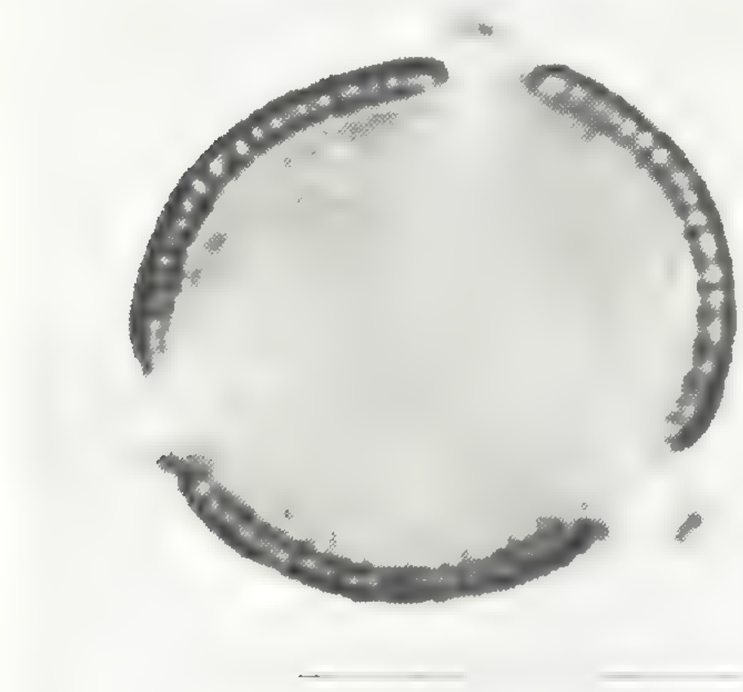

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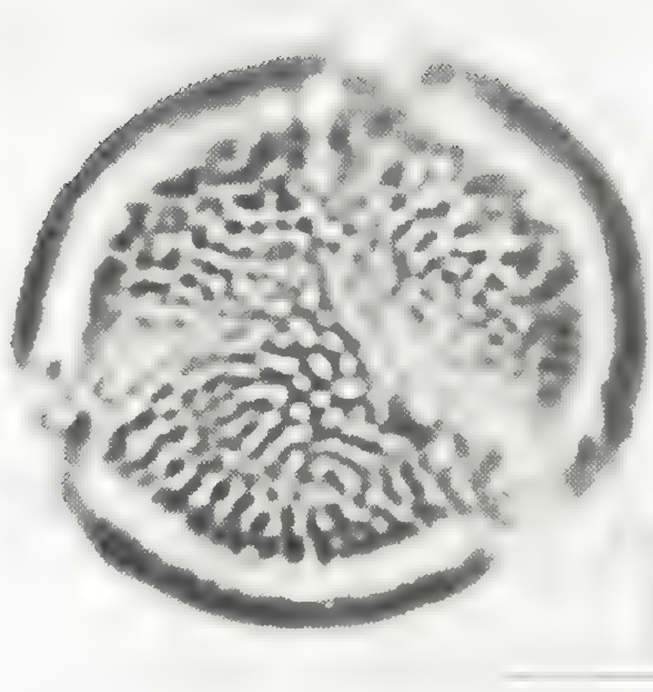

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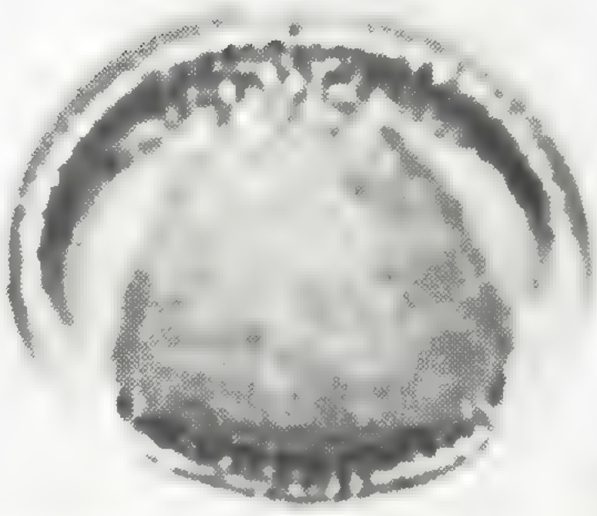

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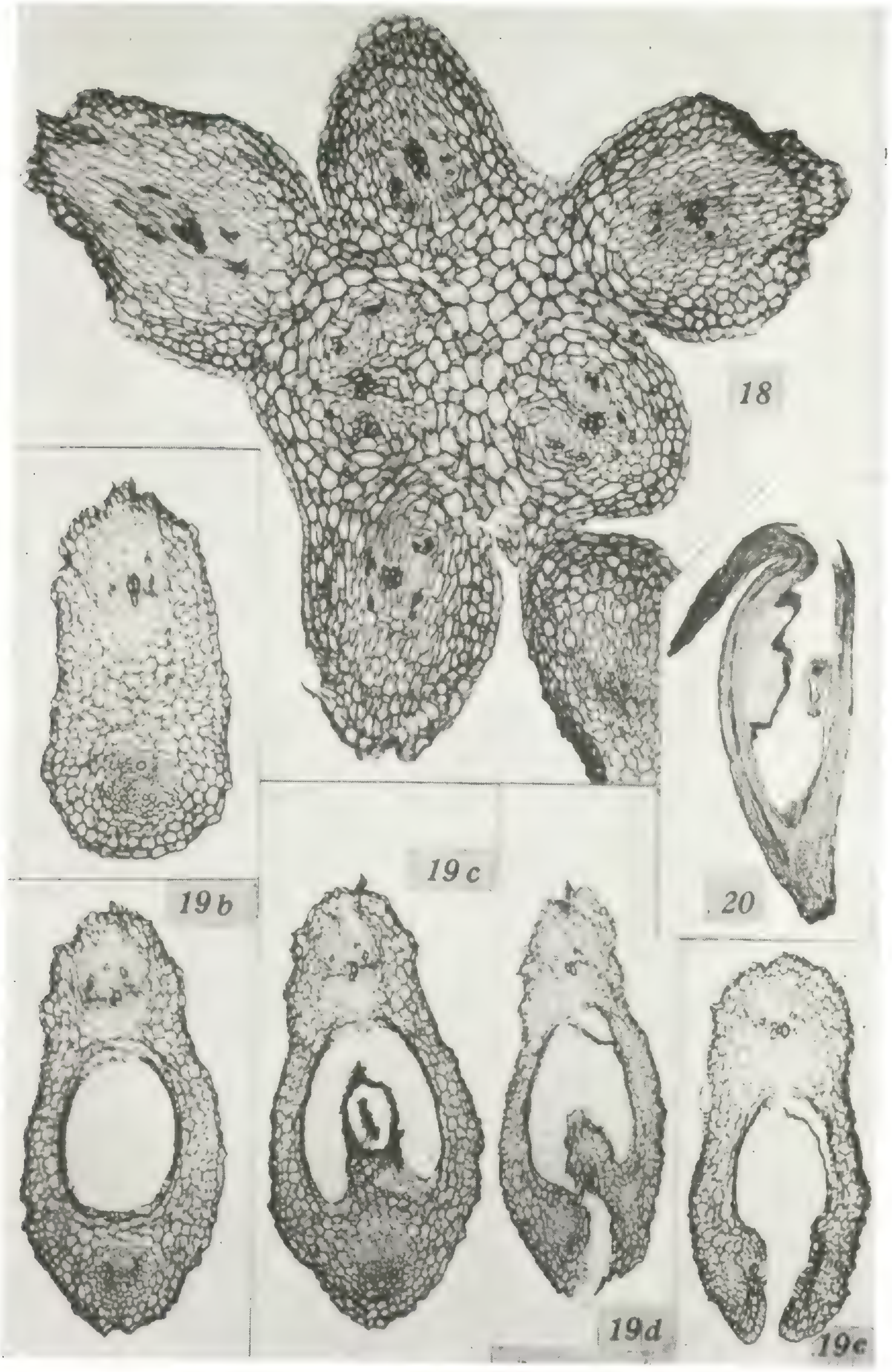

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CONIFEROUS POLLEN TYPES OF THE SOUTHERN HEMISPHERE, I. ABERRATION IN ACMOPYLE AND PODOCARPUS DACRYDIOIDES

LUCY M. CRANWELL

IN COMPARING THE POLLEN GRAINS of the Podocarpaceae with those of the Pinaceae, Mme. van Campo (1950) has recognized their common and very ancient source. In this view she has followed Prof. R. Florin (1936), who has shown how very closely aberrant grains of members of both families may approach ones normal to the Cordaitales. It is his opinion that the morphological affinity with the extinct group is strongest in the grains of certain genera of the Pinaceae. Van Campo considers that the Podocarpaceae may prove to be older, however, and points to the divergent groups persisting today. Further, she admits difficulty in deciding to which family certain types belong.

Sir Albert C. Seward (1914) ran into the same difficulty in identifying the first gymnospermous grains discovered in Antarctic deposits. He set up and defended his organ-genus *Pityosporites* in the belief that it represented abietineous grains, but soon decided that it was most probably based on podocarp material. Unfortunately, the name must be upheld as a catch-all for older bisaccate grains, of both hemispheres, which have characters common to the two families. However, as pollen studies proceed, closer identification of fossil with living types is made possible, so that a dwindling remnant of southern hemisphere "incertae" is likely to lodge, or remain, in *Pityosporites*.

Thus, despite evidence for relationship in the two major families, diagnostic differences do occur and could be exploited much more than at present for stratigraphical, distributional, and climatological studies. The work of Dr. Isabel C. Cookson, Dr. R. A. Couper, and Mr. Basil E. Balme, to mention only some who have worked in both hemispheres, is outstanding in this respect.

Particular weakness still lies in our lack of detailed knowledge of *Pinus* pollen, as contrasted with that of *Podocarpus*, or of *Cedrus*, as opposed to some of the *Dacrydia*. Records of one or the other will crop up somewhat erratically in fossil work from either hemisphere until the position is clarified. For instance, a report on Lower Miocene deposits of Silesia by Prof. Stefan Macko (1957) presses identity of his conifer types with living podocarps such as *Podocarpus dacrydioides* A. Rich. and *Dacrydium cupressinum* Soland. ex Forst. f. While I am willing to admit that genera now represented in New Zealand may also have occurred in Eurasia, I feel sure that his photomicrographs and descriptions do not clinch the matter for two reasons: the reticulate sculpture rules out a *Dacrydium*, and the presence of *Crossotheca* spores in the same deposit

suggests redeposition from older beds for the "*Podocarpus*," if closer affinity with known three-sac types cannot be proved. Neither set of microfossils exemplified by Macko comes any closer to Miocene antecedents of these species as we know them from New Zealand deposits. I mention these examples in order to stress the difficulties involved in comparing fossil podocarps of the two hemispheres, rather than to detract from Prof. Macko's main theme, which is the very real affinity between the Tethyan (or Poltavian) part of his microflora and that of Indo-Malayan vegetation of today.

Few still believe that *Pinus* and its close allies ever reached far into the Southern Hemisphere: *Pinus* today stops short in the West Indies and Guatemala, on one side of the world, and in the Sunda Islands, less than six degrees south of the Equator, on the other. On the other hand, some podocarps are found far above the Equator, mainly in the wet highlands of Central America, of Nepal, the Philippines, China, the Ryukuyu Islands, and Japan.

We are indebted to Dr. R. Florin, particularly, for purging the records, living and fossil. For South America, Antarctica, and New Zealand he has shown, for instance, that all the "Sequoia" records are false, and he has usually been able to place the macrofossils on which they were based in *Podocarpus* or *Acmopyle*.

Microfossil records usually lag behind those for macrofossils, and this is true for *Acmopyle*, one of the rarest of living conifers. Two living species, *A. pancheri* Pilg. and the very closely allied *A. alba* Buchholz, are known from the high serpentine areas of eastern New Caledonia (see Chevalier, 1957), and a third, *A. sahniana* Buchholz & N. E. Gray, from Fiji. Florin's ancient species, based on leaves and twigs, are *A. antarctica* from Seymour Island, Graham Land (Oligocene or Lower Miocene) * and *A. engelhardtii* (Eocene) from Río Pichileufu in Argentina.

An excellent note on the habitat and rich assemblage of conifers associated with *Acmopyle* is given for New Caledonia by Compton (1922). There, at 3000 ft. above sea level, the generic mixture and the ecological conditions must be very similar to those at a slightly lower altitude on Mount Te Moehau, an isolated "island," untouched by glaciation, on the Coromandel Peninsula about 40 miles east of Auckland, New Zealand. In both areas the relict forest seems to survive, as Compton puts it, through "stubborn resistance," as it is out of equilibrium with its environment.

ABERRATION IN CONIFER POLLEN GRAINS

Various authors have dealt with normal pollen grains in the Podocarpaceae, but few have described the range of aberrance in this important group, or have tried to assess its importance. I shall, therefore, confine myself in this note to its occurrence in *Acmopyle pancheri* and

* The age of the Seymour Island sediments was given by Florin (1940) and others as Eocene: recent work by the Falkland Islands Dependencies Survey indicates, however, that there are no Eocene sediments left in the region.

Podocarpus dacrydioides and shall mention the normal form only where comparison is necessary.

Hybridism and unknown factors lead to many deviations in pollen grain morphology, disturbing the familiar face, or physiognomy, of a grain. It is as though a cheek were turned in the Coniferales, in particular, when grains gain or lose bladders, reveal ancestral markings, or remain fused back-to-back with four bladders instead of two. The change of profile, so to speak, now offers new clues to cell behavior and, perhaps, to evolutionary trends. In some, the differences seem to represent a recapitulation difficult to trace except in very young or aborted grains.

Among irregularities noted for these southern genera are trisaccate grains in the normally disaccate *Acmopyle* and grains with more or less confluent sacs (bladders) or with triradiate or slashlike scars on the cap (the proximal side of the grain) in *Podocarpus dacrydioides*. Sac fusions or abortions may also occur in *Dacrydium cupressinum* and in the New Zealand species of *Phyllocladus*.

In *Acmopyle* and *Podocarpus dacrydioides*, at least, hybridism does not seem to have been involved, as the species are geographically and genetically isolated. No hybrids have been reported from *Acmopyle* or from the *Dacrycarpus* section of *Podocarpus*. Further, the frequency of irregularity is quite low, about five per cent (of 300 grains studied; Cranwell, 1940) being noted in *Podocarpus dacrydioides* and under one per cent in *Acmopyle* (with 600 grains studied). Van Campo (1950), on the other hand, reports 100 per cent aberrance in certain hybrid *Tsuga* material she investigated.

It is worth noting that few conifer hybrids have been accepted for the southern hemisphere, the late Dr. H. H. Allan (1961) giving only two groups in *Flora of New Zealand*. Both were between species with disaccate grains. Hair (1958) and Hair and Beuzenberg (1958a,b) have confirmed one of these groups in their wide surveys of chromosome numbers in the Podocarpaceae. Their material was a cross of *Podocarpus hallii* Kirk × *P. nivalis* Hook. from the closely related "hallii-totara-nivalis" complex, and it yielded counts of $2n = 36$, while the parents yielded $2n = 34$ and 38 respectively. The authors stress the importance of the evidence for chromosome inconstancy discovered in many of the 52 species, and the one hybrid, they have studied. They state (1958b) that the Podocarpaceae, instead of displaying "the unvarying basic numbers of most families of slow-growing, long-lived" gymnosperms, shows "surprising variation . . . which points both to the past and to the future." Hair (1958) adds that this "chromosomal polymorphism" is "a surprising discovery amongst the long-lived woody plants generally." Their lists show that few species with high basic chromosome numbers have trisaccate grains either regularly or occasionally. Apart from *Microcachrys* and *Pherosphaera* this condition is strong only in the groups in which Hair and Beuzenberg have demonstrated a low basic number, e.g., 10 for *Acmopyle pancheri*, *Podocarpus dacrydioides* and *Dacrydium cupressinum* ($2n = 20$).

Only a few of the trisaccate species cross the Equator, one running north

to the Philippines. All of these species belong to section *Dacrycarpus*, which has also a Chilean species described by Florin (1940) from fossil twigs. The discovery of more fossil material, as claimed by Macko (1957), would therefore represent a great extension of range for species with this pollen type. According to European reports, coniferous grains with more than two sacs are by no means common in northern deposits.

TRISACCATE GRAINS IN ACMOPYLE

The only illustrations of *Acmopyle* pollen grains to which I have had access are those of Erdtman and of Ueno. Dr. Erdtman illustrated the pollen of *A. pancheri* in 1957, promising to give the necessary text in his second volume on the gymnosperms, while Dr. Ueno gave an extremely small sketch for *A. alba* in 1960.

Thanks to Dr. Erdtman, I was permitted to see the slide on which his sketches were based; later I received fresh pollen cones from Dr. David de Laubenfels of Syracuse University, New York (*P 130*, collected on Mount Mou, New Caledonia, Oct. 9, 1957), and it was in this second collection that I noted the aberrant forms, which comprised under one per cent with three sacs and a small number only that were dwarfed, doubled, or slightly irregular in size of the sacs. The accompanying plate illustrates a trisaccate grain, together with two typical disaccate grains, seen in distal and lateral views (FIGS. 1–3).

It should be noted that the three sacs are in perfect balance and condition (FIG. 1), but the exine of the corpus (body of the grain) is very thick and is embayed between the sacs. As in normal grains, the puffed bladders are attached by narrow bases and lie wholly on the distal surface of the grain.

Most of the irregular grains were smaller than the normal ones, but the overall measurement, with sacs included, was little smaller, being about 62μ. No grains were broken, but several (normal) had shed a sac very cleanly, possibly due to the rigors of acetolysis during the preparation of the sample. The tendency to shed seems stronger than in other podocarp pollen types: it may thus be significant that sacless grains of this type occur rather freely in Upper Cretaceous Antarctic sediments which I am studying at present. No bladders like those of *Acmopyle* have been recognized, however, although many fragments have persisted.

SOME FOSSIL OCCURRENCES OF TRISACCATE TYPES

Occurrences in older floras will not be discussed in detail here, but it is worth noting a second trisaccate type also found by the author in the Antarctic samples. Deviations from the coniferous types suggest that it may have been shed by a pteridosperm.

The trisaccate condition is certainly very old, though not as old, it seems, as some of the types with enveloping or cingulate sacs. In *Podocarpus dacrydioides*, at least among the podocarps, a deviant takes the

form of this more ancient fused sac, comparable with those sometimes developed in *Pinus sylvestris*, according to reports by Eneroth (see Florin, 1936). Such grains occurring in podocarps, pines, and their allies, even if rarely, seem to give good support for Florin's views on the common ancestry of these groups in the Cordaitales.

Trisaccate grains occur rather sparingly among the Abietineae in both fossil and living material. They occurred also in extinct groups the affinities of which are little understood. Couper (1958) has reported them, for instance, in frequencies of one in a thousand for the normally bisaccate *Caytonanthus arberi* (Thomas) Harris, a member of the Caytoniales which lived in the Mesozoic period in Britain.

The nomenclature for these types is especially difficult: some are lumped in *Trisaccites*, or, if a comparatively recent origin is suspected, in an organ-genus suggesting affinity, e.g., *Podosporites*. Where there is a continuous record for a species, as for *Podocarpus dacrydioides* in New Zealand, the affinity can well be claimed, but even for this distinctive type the record does not yet go back beyond the Tertiary.

TRIRADIATE SCARS IN PODOCARPUS DACRYDIOIDES

The triradiate scar, the mark of contact with other grains of a developing tetrad, occurring always on the proximal or cap side, is rarely noted in conifers, and has never been confirmed for any angiosperm, although *Coprosma macrocarpa* Cheesem., for one, has a polar marking which mimics a scar. Wodehouse (1935) has illustrated a scar for *Abies nobilis* Lindl., for instance, and has stated that it is a "diagnostic character when found but it is generally very faint and difficult to see." Florin (1936) reports much the same thing for *Cordaianthus* and illustrates a grain with a small, compact scar.

Ueno (1957) has given the only reports of a scar in *Podocarpus dacrydioides*, as far as I know. His illustration I noted with admiration and a mild chagrin, as I had never observed one of these scars in the many grains I have worked with, living or fossil; the only deviations I had seen were frillings and fusions of the sacs. I was fortunate, therefore, on October 25, 1958, to be able to collect young cones, which I took from a small tree, not long out of its juvenile stage, by the Waitakere Stream not far from Auckland. In this material I found an abundance of scars, as well as broad slash-like markings not mentioned by Dr. Ueno.

In *Podocarpus dacrydioides*, the scar lies in the middle of the body of the grain, sending its long, untapered arms out almost to the equator where each comes symmetrically and abruptly to a point. As will be seen (FIGS. 6, 7), the arms are broad, both margins and surfaces being clearly delimited. By comparison with such ancient types as *Illinites* Kosanke and *Fuldaesporites* Leschik (as illustrated in Potonié, 1958, *Taf. 7, 62* and *Taf. 9, 91*, respectively), or with modern fern types, such as the spores of *Adiantum*, this is a large and magnificent scar. It does not run into and fuse with the ridge encircling the equator, as Ueno reports for *Tsuga*. I

agree with him, however, in his suggestion that only young grains are likely to show the triradiate marking to advantage.

IRREGULARLY SCARRED GRAINS

The chief aberrations in this species, and the ones most likely to be of importance, are the slash-like strips running singly on in pairs across the proximal surface. Their "selvage" margins are wide and calloused (FIGS. 9, 10) and thus suggest rigidity, rather than distensibility, of the wide and delicate membrane of the distal surface. This latter is usually spoken of as the "furrow," although it is not homologous with the furrow of most of the angiosperms.

Several fossil pollen genera are characterized by rather similar rifts (see Potonié, 1958, *Taf. 7, 63, 64*, and especially Balme and Hennelly, 1955). These are disaccate grains, the gashes tending as a rule to run straight and at right-angles to the side furrows on the other side of the grain. In *Podocarpus dacrydioides*, likewise, the seemingly haphazard pattern of rifts may be determined by the geography of a triangular, rather than an elongate, furrow area. In a "normal" young grain, the arms of the *perfect* triradiate scar will run toward the apex of each subtending air sac, as it would to the three angles formed on the amb of trilete fern spores. The disturbance of the abnormal grain, whatever its cause, may thus lead to gross thickenings and erratic trends in the trisaccate types.

In "Lueckisporites" of Balme and Hennelly (1955) a straight gash occurs together with lesser parallel striation. Such grains are especially important in members of the Gondwana Flora (see also Pant & Nautiyal, 1960) but have not yet been reported from Gondwana deposits in New Zealand. Their association with delicate triradiate crests in some sacless microspores described by the Australian workers suggests that their early function was separate from that of the scar. It will be interesting to discover for modern conifers what relationship the heavy gashes have to both the triradiate scar and the ancient striations.

ACKNOWLEDGMENTS

I offer my thanks to Dr. Gunnar Erdtman, of Stockholm, and to Dr. David de Laubenfels, of Syracuse University, New York, for sharing their *Acmopyle* material with me, and to my nieces, Miss Eleanor Ann Cranwell and Miss Norma L. Cranwell, of Henderson, New Zealand, for helping collect the young *Podocarpus dacrydioides* cones near their home in 1958. I also have had helpful correspondence concerning gymnosperm pollen morphology with Dr. Vishnu-Mittre, of the Birbal Sahni Institute of Palaeobotany, Lucknow, India, and with Dr. Jitsuro Ueno, of Osaka City University, Osaka, Japan. Finally, I am grateful to Dr. Elso S. Barghoorn, of Harvard University, for allowing me to browse in his pollen library during the summer of 1960.

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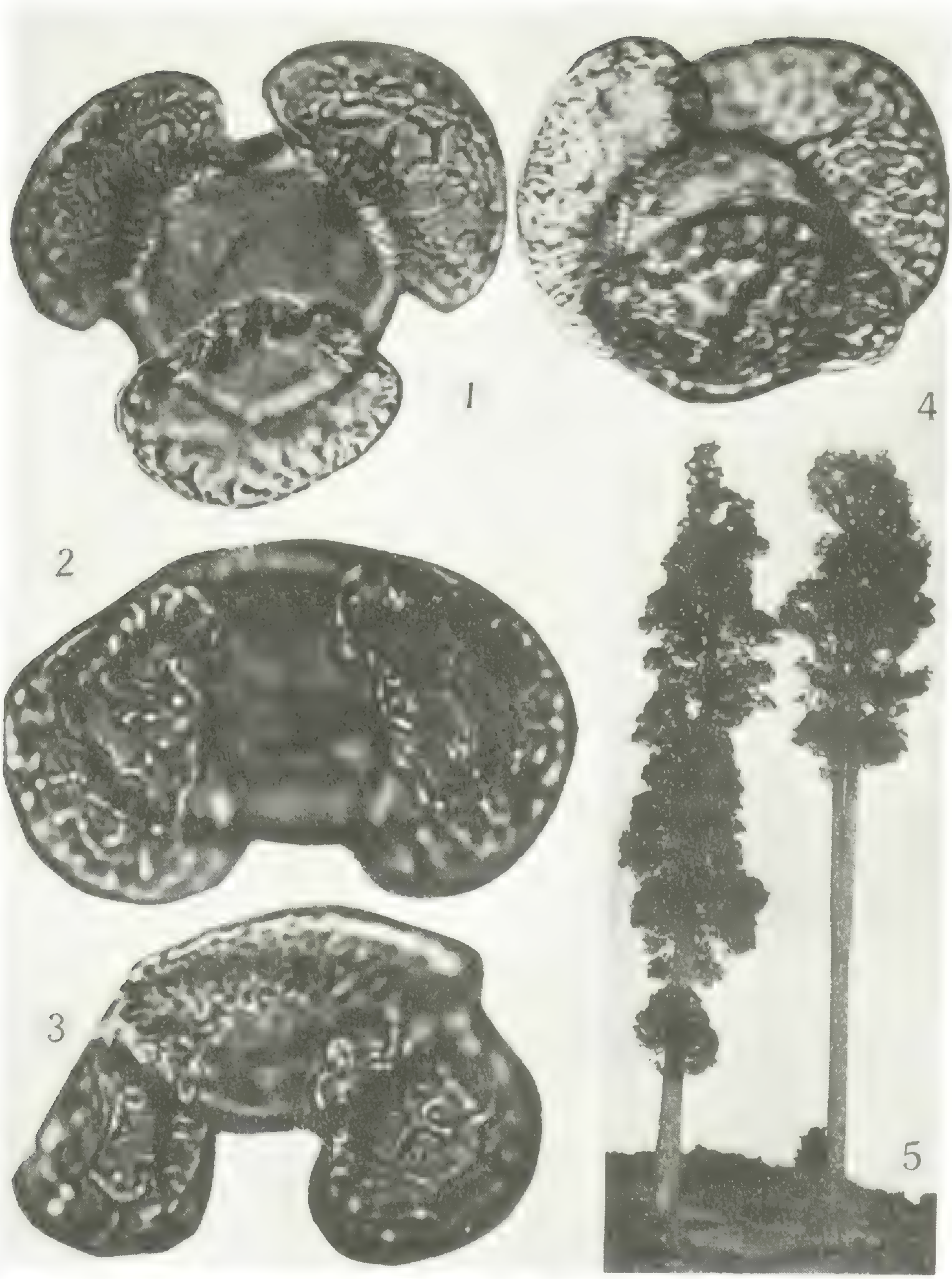
EXPLANATION OF PLATES

PLATE I

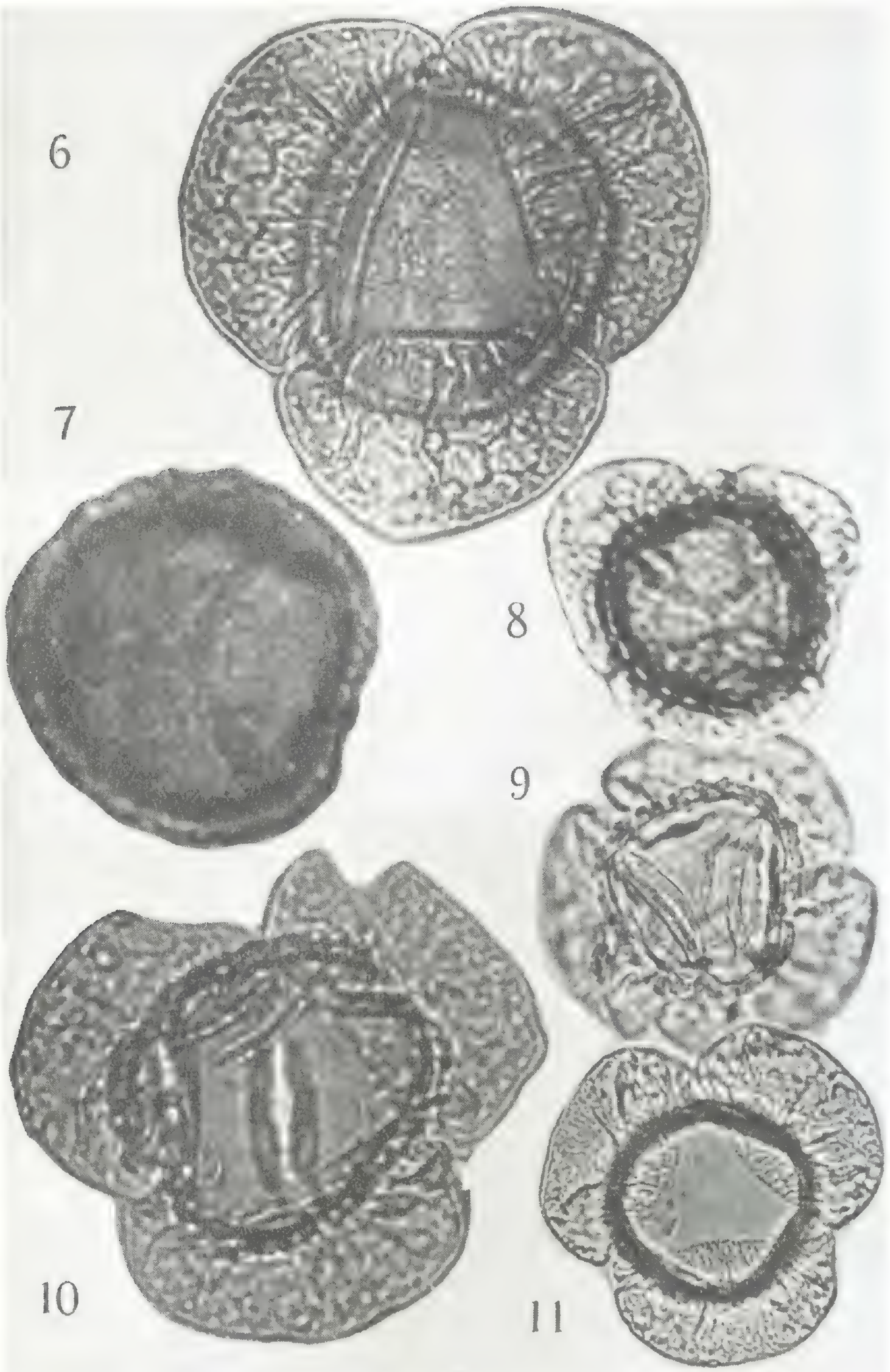
FIGS. 1–5. *Acmopyle* and *Podocarpus*. FIGS. 1–3. Photomicrographs of pollen grains of *Acmopyle pancheri*. 1, Trisaccate grain, 62μ, showing the symmetric and widely spaced sacs, the lowest being turned inward slightly toward the germinal area or "furrow." 2, Disaccate grain, 69μ, showing distal or "furrow" side of grain. 3, Disaccate grain, 69μ, in lateral view showing the puffed sacs on their narrow bases, their slight projection beyond the body of the grain, and their open reticulation of the sacs [Material: *De Laubenfels P130*; pollen preparation, p5 (acetolysed)]. FIG. 4. Photomicrograph of pollen grain of *Podocarpus dacrydioides*. Normal grain in slightly oblique view, the sacs crowd closely together above the rounded "furrow" area; 65μ. [Material: *L. M. & E. A. Cranwell*; pollen preparation S768 (acetolysed)]. FIG. 5. Very old trees of *Podocarpus dacrydioides* ("Kahikatea") isolated after felling of forest around them; King Country, New Zealand. Photographs by author.

PLATE II

FIGS. 6–11. Photomicrographs of pollen grains of *Podocarpus dacrydioides*. 6, Distal view of normal grain (possibly not fully mature), 65μ, showing attachment of the wide bases of the sacs on the large triangular "furrow" area. 7, 8, Young grains, 46 μ, showing the broad triradiate scars on their cap (proximal) side — bladders have been trimmed away in fig. 7 leaving only body or corpus of grain. 9, 10, Aberrant grains with open wound-like scars. 11, Normal grain overlapping an aberrant one (10), both about 70 μ.



CRANWELL, CONIFEROUS POLLEN TYPES, I



CRANWELL, CONIFEROUS POLLEN TYPES. I

STUDIES IN THE THEACEAE, XXXIII
VARIATION IN THE FRUIT OF TERNSTROEMIA KWANGTUNGENSIS

CLARENCE E. KOBUSKI

COMPLETE DIAGNOSES of taxa in the genus *Ternstroemia*, like those of any other genus, should include the descriptions of both flowers and fruit. Considering that the flowers of this genus are either dioecious, androdioecious, or occasionally hermaphroditic and that flowers seldom are collected at the same time as the fruit, one may see how inadequate a description based on a single herbarium specimen must be. In the species discussed below the flowers are still unknown. The fruiting material available to the original authors (two names are involved) was insufficient for a complete diagnosis of the fruit. However, it so happens that in *Ternstroemia kwangtungensis* the leaf characters seemed outstanding enough at the time of its description to set it apart from all other Chinese members of the genus. The fruit is widely variable, and it is with this extreme and unusual variation, in contrast to the uniformly 2-loculate condition of most other Asiatic species, that the present paper is concerned.

In 1918, E. D. Merrill described an interesting new species of *Ternstroemia* from Kwangtung Province, China, as *T. kwangtungensis*. He obviously never realized at the time — or later — how distinct and unusual the species actually would turn out to be. The type collection was made by Merrill himself, and, although it was a rather wretched specimen, Merrill with his keen eye for novelties recognized it as different from any *Ternstroemia* previously described from China. What attracted Merrill, I am sure, was the heavy, subrotund, shiny, coriaceous leaves and the broad, very thick petioles, with the overall appearance of a stiff fan or paddle. The fruit was immature, and as such he dismissed this character. Since then several workers have identified Kwangtung material in the Arnold Arboretum herbarium as belonging to this species, but, upon close observation, none of the specimens truly resembles Merrill's isotype which had been deposited at the Arnold Arboretum.

Since the isotype available (*Merrill 11013*) was so sparse (one attached and one unattached immature fruit) I had hesitated to dissect the material until absolutely necessary. However, when a dissection was finally made of the unattached fruit I discovered that it was so very young in development that it was still in the advanced ovulate stage.

There were five locules. However, of these, only three were fertile and contained respectively three, two, and two ovules. The inside surface at the apex of the locules where the ovules were attached was dark red, smooth, and shiny. In the two intervening spaces (or sterile locules) such was not the case, these being filled with spongy tissue. Two of the

fertile locules were adjacent to each other and were separated by a single septum. On each side of these two adjacent fertile locules was a sterile locule with the third fertile locule between the two sterile locules. It is quite likely that in the maturation of the fruit the fully developed seeds may fill the fruit completely, thereby eliminating the sterile locules, for in this genus it is not unusual to find that the septa separating the locules have been broken down by the developing seeds.

A second specimen which appeared to belong to this species, *Tsang 25486*, was found among our unidentified material. This specimen also had only two fruits. A single dissection of a fruit of this second specimen showed it to be 3-loculate with the three locules clearly taking up the entire fruit, with no intervening spaces. The seeds numbered seven and were arranged four, two, and one in the three locules.

A short while ago, I was surprised to find that H. T. Chang (Zhongsan Daxue Xuebao, Ziran Kexue [Bull. Sun Yatsen Univ. Nat. Sci.] 2: 25. *pl. 7*. 1959) had described a new species, *Ternstroemia subrotundifolia*, from Kwangtung and had cited *Tsang 25486*, already mentioned above, as the type of his species. What startled me even more was that Chang mentioned the fruit as 5-locular with a single seed in each locule.

Since the Tsang collection was made under the sponsorship of the Arnold Arboretum and is not yet distributed, four duplicates of *Tsang 25486* have been available for my study, thus affording an opportunity to make several dissections of the fruit without destroying the value of the specimens, which, after all, are isotypes of Chang's species. My findings are recorded in the table which follows:

MATURE FRUIT OF *Tsang 25486*

NO. OF LOCULES	NO. OF SEEDS	SEEDS IN LOCULES
3	7	4–2–1
3	6	2–2–2
3	5	2–2–1
3	5	2–2–1
4	7	1–2–2–2
4	5	2–1–1–2
5	7	1–2–1–2–1

In the seven dissections made from this single collection, the fruits were found to have either three, four, or five locules, with three the dominant number. The total number of seeds for each fruit varied very little, usually five or seven with only one fruit showing six seeds, two to each of the three locules.

Chang in his description (both Latin and Chinese) gives the fruit as 5-locular, with a single seed in each locule, an arrangement which I did not find in any of my observations. Since Chang was working with a duplicate of the same collection (*Tsang 25486*) with which I have worked, we can only assume that his finding was made from a single dissection and that his finding, although quite ideal, is mere chance.

The style, being quite short, may persist unbroken into the fruit. It is

quite thickened at the base and then divides into three, four, or five short branches. In the dried fruit, the branches are usually pressed down, brittle, and difficult to separate. I do feel, however, from the examination of the material available that the number of branches of the style is the same as the number of locules in the ovary or fruit, a conclusion which is logical rather than observationally accurate.

This occurrence of varying numbers of locules in the fruit obviously shows that an evolutionary change is taking place. In all of the material of *Ternstroemia* which I have studied from the Eastern Hemisphere I have found only one other variant from the 2-loculate ovary and fruit. *Ternstroemia patens* (Korthals) Choisy, a very rare plant of Sumatra, is 1-loculate in both flower and fruit. Furthermore, a single pendulous ovule is found in the ovary, and a single seed in the fruit. One may consider this the extreme in development.

It is possible that *Ternstroemia kwangtungensis* represents a more primitive taxon of the genus in transition from a 5-loculate to a 2-loculate state. The two sterile locules in the undeveloped fruit of the type might be considered further evidence of this transition.

As far as I know, this taxon has been collected only three times and only in Kwangtung. The type was collected by Merrill at Lofaushan, an area well known botanically, about 60 miles east northeast of Canton (23° 15′ N, 114° 8′ E). Tsang (*25486*) collected the type of *Ternstroemia subrotundifolia* at Linfashan (22° 59′ N, 115° 20′ E), which is about 75 miles southeast of the Lofaushan. Both of these specimens I have examined. Chang cited a third specimen (*H. Tse 608*) collected at Yingtak (24° 10′ N, 113° 5′ E), located about 80 miles west-northwest of Lofaushan. These three collections extend over a distance of 150 miles. In well-collected Kwangtung, it seems strange that it has not been encountered more often, since Tsang commented in his field notes that it was "fairly common."

Below is recorded a nomenclatural treatment with an amplified description.

Ternstroemia kwangtungensis Merrill, Philipp. Jour. Sci. Bot. **13**: 148. 1918. — Melchior, Nat. Pflanzenfam. ed. 2. **21**: 141. 1925.

Ternstroemia subrotundifolia Chang, Zhongsan Daxue Xuebao Ziran Kexue (Bull. Sun Yatsen Univ. Nat. Sci.) **2**: 25. *pl. 7*. 1959 — *syn. nov.*

DISTRIBUTION: China (Kwangtung).

KWANGTUNG: Loh Fau Mountain (Lofaushan), in damp, forested gorge, alt. ca. 300 m., *E. D. Merrill 11013* (A, lectotype* of *Ternstroemia kwangtungensis*), Aug. 29, 1917; Hai-fung Distr., Lin Fa Shan, Pak Shui Chai, *W. T. Tsang 25486* (A, isotype of *Ternstroemia subrotundifolia*), Aug. 15–24, 1935 (scattered shrubs, fairly common, 3 ft. high; fruit red).

* The original holotype, deposited in the herbarium of the Philippine Bureau of Science, was destroyed during the Second World War, hence this designation of a lectotype

Shrub or small tree, 1–4 m. high. Branches and branchlets stout, 5–7 mm. diameter, rugose, reddish brown, the petiolar scars prominent. Leaves thick-coriaceous, elliptic-ovate to suborbicular, 7–9 cm. long, 3–5 mm. wide, rounded or obtusely acuminate at the apex, obtuse or broadly cuneate at the base, dark green above, tawny or reddish brown and dark-punctate beneath, the margin glandular-denticulate, especially along the upper half on younger leaves, less obvious on the older leaves, the midrib canaliculate above, plane or lightly elevated below, the primary veins 5–7 pairs, quite indistinct, curving upward near the margin, the petiole robust, 1.5–2 cm. long. Flowers not seen. Fruit axillary, solitary, depressed-globose, 1–1.6 cm. long, 1.2–1.8 cm. diameter, 3–locular, occasionally 4- or 5-locular, 5–7-seeded, the seeds conduplicate, 7–8 mm. long, ca. 6 mm. diameter, covered with a tawny, mealy aril; fruiting style short, thick, 1–2 mm. long, branching near the apex, the style branches apparently equalling the locules in number, each branch topped by a small capitate stigma; fruiting pedicel stout, 1–1.5 cm. long, ca. 3 mm. diameter; persistent bracteoles 2, opposite, immediately below the calyx, broadly ovate or deltoid-ovate, ca. 3 mm. long, 4–5 mm. wide at the base, the margin scarious; persistent calyx-lobes rounded, ca. 6–7 mm. long and wide.

THE CORRECT NAMES FOR "DIOSPYROS EBENASTER"

RICHARD A. HOWARD

THE NAME *Diospyros ebenaster* Retzius has been commonly applied to trees from the West Indies, Central America, South America, and many areas of tropical Asia. The tree and its fruit are known as black apple or sapotte negro. Collectors in both the New and the Old World have suggested that certain of their collections may represent cultivated plants, but some have considered the tree to be indigenous in all of the area cited. The occurrence of early historical records of this plant in botanical gardens suggests that its use by man may have been the basis for its introduction into new areas. It is reported to have an edible fruit, but either the quality of the fruit varies, or else individuals vary in their acceptance of its palatability, if one is to believe the conflicting reports. In both hemispheres, parts of the plant are used by the native peoples as a fish poison.

The peculiarly widespread distribution of this species has made it difficult to determine the country of origin. Scott (Kew Bull. 1915: 65. 1915), who reviewed thoroughly the existing literature regarding this species, pointed out that "the bulk of the evidence, then, points to *Diospyros Ebenaster* being introduced into the East Indies." He also pointed out that Urban (Symb. Ant. 4: 485. 1910) "is apparently convinced that the tree is a native of the West Indies" and that Duss' (Fl. Phan. Ant. Fr. 390. 1896) "discoveries leave us no doubt whatever, for he found the tree in various wild places" in Guadeloupe. Scott concluded that all records from Brazil seemed to indicate that the tree was cultivated, and he summarized his findings by saying that "from the evidence we have collected, therefore, we must conclude that the natural habitat of *Diospyros Ebenaster*, Retz., is in the West Indies. With regard to Mexico, it is evident from the references quoted . . . that the tree must have existed there for at least three centuries . . . It is very probable that the tree was introduced into Mexico by the Spaniards, but if this be correct, the introduction must have taken place at a very early date."

In Montserrat, I have been able to examine trees, called the black apple, which would be referred to *Diospyros ebenaster* and have also seen herbarium specimens of this plant from Cuba, Hispaniola, Puerto Rico, Guadeloupe, Marie Galante, and Dominica in the West Indies. Excluding the collections from Cuba and Haiti, not one of the sheets suggests a plant under cultivation, or anything other than a component of the natural vegetation. The trees in Montserrat were in native woodland in areas which have never been heavily cultivated, having been preserved historically as watershed areas. However, a total of seventeen collections from Mexico, British Honduras, and Costa Rica has been studied, of which three specimens are clearly indicated as being from cultivated plants. From these recent collections one might draw evidence in support of Scott's

conclusion that *D. ebenaster* is a native of the West Indies which has been introduced into Mexico and Central America. However, a study of the material from these two geographic areas indicates that two species are represented, and that it is the Mexican-Central American population which has been introduced into the Pacific area, Cuba, Haiti, and Brazil. The Mexican-Central American plants have oblong-lanceolate leaf blades evenly tapered at both ends or rounded at the base and bluntly acute at the apex. The venation is ascending and arcuate, anastomosing near the margin. The fruit is borne on a stout pedicel averaging 5 mm. in thickness and the fruit is 5–6 cm. in diameter. The fruiting calyx is 4–5 cm. in diameter with large, broadly ovate lobes, the whole calyx appearing undulate or wavy.

In contrast to this, the ample material obtained for the purpose of studying variation in Montserrat, supported by additional collections for the other islands of the Lesser Antilles, has, on the average, smaller leaves which are elliptic-oblong, narrowed at the base, and rounded, obtuse, or often emarginate at the apex. The blades appear to have had a heavier texture than those of plants from Central America. The venation is ascending, but is not arcuate until the veins bifurcate and anastomose near the margin of the blade. The fruit is smaller, averaging 3 cm. in diameter, although it is noted on *Hodge 2091* that the "fruits grow to 3 × the size of this specimen." More significant, however, is the shape and size of the fruiting calyx which, in the largest specimen available, is 1.5 cm. in diameter and almost square in surface view, with the calyx lobes scarcely indented and the whole calyx flat and coriaceous. Adequate flowering material is lacking from both geographic areas.

The evidence thus indicates that there are in the New World two species which have passed as *Diospyros ebenaster*. Herbarium specimens available from the Philippines and Malaysia may be clearly assigned to the taxon from Central America. Both species require names.

Bakhuizen van den Brink, in a revision of the Malaysian Ebenaceae (Bull. Jard. Bot. Buitenzorg III. **15**: 316–320. 1938), considered *Diospyros ebenaster* Retzius to be a probable synonym of *D. ebenum* and renamed the material generally called *D. ebenaster* as *D. nigra* (Gmel.) Perrottet. Bakhuizen considered this species to be indigenous to the Antilles, Brazil, Mexico, Texas, and Florida, and both spontaneous and cultivated in the Philippines, Celebes, Mauritius, Réunion, Ceylon, and Malacca. In taking up *D. nigra*, Bakhuizen gave an extensive citation of both pre-Linnaean as well as post-Linnaean literature. The basic species cited and the supporting literature references, here partly rearranged, are the following:

Diospyros nigra (J. F. Gmel.) Perrottet, Mém. Soc. Linn. Paris **3**: 113. 1825.

Sapota nigra J. F. Gmelin, Syst. Nat. ed. 13. **2:** 750. 1791.
D. digyna Jacq. Hort. Schoenbr. **3:** 35. *pl. 313.* 1798.
D. revoluta Poir. in Lam. Encycl. Méth. Bot. **5:** 435, no. 18. 1804.

D. obtusifolia Humb. & Bonpl. ex Willd. Sp. Pl. **4:** 1112. no. 17. 1805; HBK. Nov. Gen. et Spec. Pl. **3:** 253. *pl. 247.* 1818.
D. sapotanigra A. DC. Ess. Prop. Méd. Pl. ed. 2. 200. 1816.
D. sapota Roxb. Flor. Ind. ed. 2. **2:** 535. 1832.
Sapota nigra Blanco, Fl. Filip. 409. 1837.
D. nigra Blanco, Fl. Filip. ed. 2. 211. 1845.
D. membranacea A. DC. in DC. Prodr. Syst. Nat. 8: 227. no. 20. 1844.
D. laurifolia A. Rich. Fl. Cub. in Ramon de la Sagra, Hist. Cuba **11:** 86. 1853; Ramon de la Sagra, Icon. Fl. Cub. Pl. Vasc. *pl. 55.* 1863.
D. brasiliensis Mart. ex Miq. in Mart. Flor. Bras. **7:** 5. *pl. 2, fig. 2.* 1856.
D. Ebenaster Hiern, Monogr. Eben. in Trans. Cambr. Phil. Soc. 12(1, 2): 244. no. 125. 1873, non Retzius.

Although two species are involved in the description and in the references given by Bakhuizen, the name he has chosen cannot be used for either one. Apparently Bakhuizen did not see the reference he used for Perrottet's eipthet, for Perrottet did not transfer Gmelin's name, but described a new species. The article by Perrottet is short and reads "DIOSPYROS *nigra* Perr. Espèce nouvelle des Philippines que les créoles de Mascareigne appellent *Sapot negro*; son fruit est très-gros, assez semblable, pour la forme, au melon cantaloup galeux" (Mém. Soc. Linn. Paris 3: 113. 1825). Perrottet further indicated that the plant was cultivated in the Mascarene Islands and at Cayenne.

Gmelin (Syst. nat. ed. 13. 2: 750. 1791) in contrast, had based his description on the phrase "Sapotte negro" used as a common name, although given with a description and illustration, by Sonnerat in his *Voyage à la Nouvelle Guinée* (p. 45. *pl. 14–16.* 1776) for a plant from the Philippines. Although Perrottet, Gmelin, and Sonnerat were all describing the same species, Gmelin's *Sapota nigra* cannot be transferred to *Diospyros* because of Perrottet's publication. It is also of interest to note that the same plant from the Philippines was described as new by Blanco as *Sapota nigra* (Fl. Filip. 409. 1837) and later transferred to *Diospyros* as *D. nigra* (Blanco) Blanco (Fl. Filip. ed. 2. 211. 1845).

The earliest available name for the Mexican-Central American plant introduced in the Pacific Islands is *Diospyros digyna* Jacquin, based on a plant grown in Austria from seeds collected in the Celebes. No type specimen of this species exists at Vienna, but the original ink drawing used in preparing the published illustration (Hortus Schoenbrunnensis 3: 35. *pl. 313.* 1798) is preserved in the Vienna herbarium. The illustration must suffice to typify the species. The drawing of the branch showing the leaves, their venation, and the position of the flowers, matches fairly well the Pacific Island material of "Sapote negro," as well as material from Mexico and Central America. The calyx, illustrated by Jacquin, appears to be that of a staminate flower. The pistil has a pubescent ovary typical of that found in recent collections examined from the Old World as well as Central America. The Jacquin illustration shows two styles, as indicated in the specific epithet, but a comparable abnormality has not been located in the staminate flowers examined. Certainly the majority of the char-

HOLOTYPE OF DIOSPYROS MEMBRANACEA A. DC. FROM MAURITIUS. (Prodromus Herbarium, Geneva.)

acteristics to be seen in the illustration are pertinent to the Central American species. The common name of "false mangosteen" may also be considered as support. The correct name and the synonymy of this species appears to be:

Diospyros digyna Jacq. Hort. Schoenbr. **3**: 35. *pl. 313*. 1798.

Sapota nigra J. F. Gmelin, Syst. Nat. ed. 13. **2**: 750. 1791.
Diospyros obtusifolia Humb. & Bonpl. ex Willd. Sp. Pl. **4**: 1112. 1805; HBK. Nov. Gen. Sp. Pl. **3**: 253. *pl. 247*. 1818.
Diospyros sapota Roxb. Fl. Ind. ed. 2. **2**: 535. 1832.
Diospyros sapotanigra A. DC. Ess. Prop. Méd. Pl. 200. 1816.
Diospyros nigra Perrottet, Mém. Soc. Linn. Paris. **3**: 113. 1825.
Sapota nigra Blanco, Fl. Filip. 409. 1837, non Gmelin.
Diospyros membranacea A. DC. Prodr. **8**: 227. 1844.
Diospyros nigra (Blanco) Blanco, Fl. Filip. ed. 2. 211. 1845, non Perrottet.
Diospyros laurifolia A. Rich. Fl. Cub. in Ramon de la Sagra, Hist. Cuba **11**: 86. 1853; Ramon de la Sagra, Icon. Fl. Cub. Pl. Vasc. *pl. 55*. 1863.

Several of these synonyms have not been discussed above. *Diospyros obtusifolia* was based on a plant from Mexico and clearly is to be referred here. *Diospyros sapota* Roxb. has the same basionym as *Sapota nigra* Gmelin in a Sonnerat reference to a plant from the Philippines. *Diospyros sapotanigra* A. DC., attributed to Mexico, is a nomen nudum. *Diospyros laurifolia* A. Rich. is well illustrated and, although from Cuba, clearly refers to the Central American species and must represent an introduced plant. *Diospyros membranacea* A. DC. was based on a collection from Mauritius. A photograph of the holotype which was made available through the kindness of Dr. Charles Baehni indicates that this species is also to be referred here. Dr. R. E. Vaughan, of Reduit, Mauritius, has written me, "I have seen a specimen in the Paris Herbarium collected by Commerson in Mauritius C. 1769 so it has been here for a long time. It appears in a list of plants growing in the Botanical Gardens, Pamplemousses in 1785 under the name 'Sapotte negro des Molucques.' "

I have seen no specimens determined as *Diospyros brasiliensis* which Miquel attributed to Martius (Flor. Bras. **7**: 5. *pl. 2, fig. 2*. 1856), but the species was collected by Pohl in Brazil and, judging from the illustration, may well be assigned to the synonymy of *D. digyna*.

Bakhuizen's reference to *Diospyros nigra* occurring in Texas and Florida was not supported by cited specimens, and I have seen no cultivated specimens from either state.

The date or the path of the introduction and the distribution of the Mexican-Central American *sapote negro* to the Pacific area cannot be determined. It is clear, however, that the plants of the Pacific area called *Diospyros ebenaster* Retzius by many authors and *D. nigra* by Bakhuizen originated in Mexico-Central America and are correctly called *D. digyna* Jacq.

The native plant of the Lesser Antilles (with one record from Puerto Rico) is distinct, although previous authors have placed it with the species just discussed. The correct name for this plant is *Diospyros revoluta* Poiret (Lamarck, Encycl. Méth. Bot. **5**: 435. 1806), and it was originally described as follows:

Diospyros foliis obovatis, obtusis, glaberrimis; pedunculis solitariis, reflexis; calicibus profunde lobatis. (N).

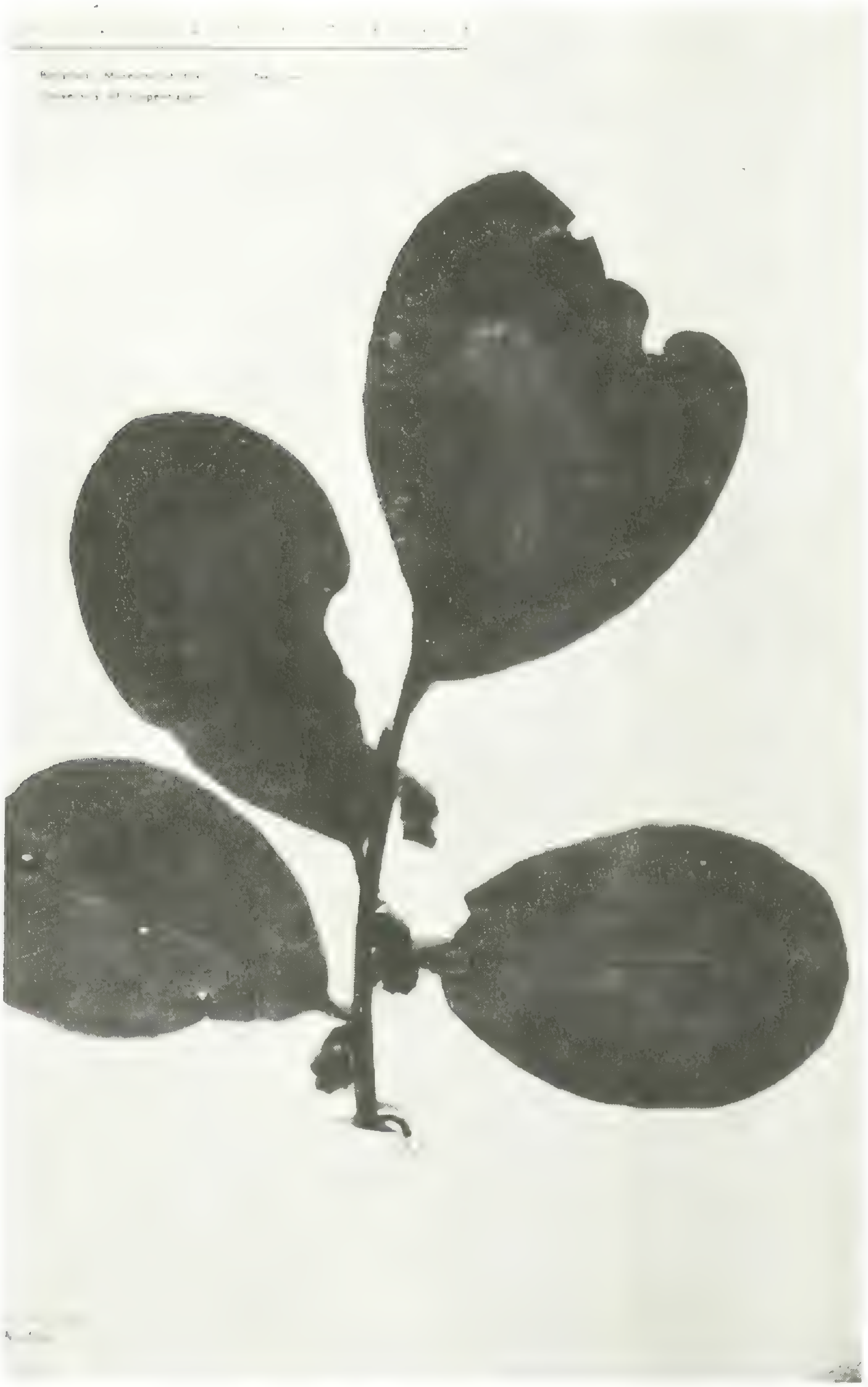
Les tiges des jeune rameaux sont striées, presqu'anguleuses, munies de feuilles alternes, pétiolées, coriaces, très-glabres, luisantes, ovales, rétrécies, aiguës à leur base, arrondies à leur sommet, longues de quatre à cinq pouces, larges au moins des deux, supportées par des pétioles très courts, marquées de nervures confluentes à leurs bords. Les fleurs sont axillaires, solitaires, munies de pédoncules courts, fortement recourbés: leur calice est glabre, persistant, coriace divisé en quatre grands lobes profonds, arrondis. Les quatre divisions du tube de la corolle sont équalement réfléchies en dehors sur le jeune fruit. Celui-ci est un baie glabre, arrondie, d'une médiocre grosseur.

Cette plant est originaire de l'Amérique méridionale. Elle a été communiquée par M. Vahl à M. Jussieu. [symbol for a shrub] (V. S. fruct. in herb. Juss.)

I have been unable to secure information regarding the existence of a specimen in the Jussieu Herbarium in Paris. In the Copenhagen herbarium there is a specimen studied by Vahl which was collected by Ryan in Montserrat. Associated with the specimen is a complete diagnosis in Latin, with the name *Diospyros revoluta*. The specimen was originally identified as *D. tetrasperma* Sw. and then considered to be a different and new species. Vahl sent the information, and perhaps a specimen, to Jussieu. The specimen and both the Latin and the French diagnoses agree with the Lesser Antillean plants commonly known as *D. ebenaster* Retzius. *Diospyros revoluta* apparently has not been transferred by man to other areas, and the following records appear to represent native plants of the West Indies.

DOMINICA: Calibishie, *W. H. & B. T. Hodge 3177* (GH); Laudat, *W. H. Hodge 2091* (GH); between Salybia and Concorde Valley in Carib Reserve, *W. H. & B. T. Hodge 3282* (GH); Pointe Rond to Milton Estate, *W. H. & B. T. Hodge 2676* (GH). MARIE GALANTE: Pointe de Folle Anse, *Proctor 21068* (A). MONTSERRAT: Without specific location, *Ryan* (type); Salem, *Shafer 559* (US), *Proctor 18897* (A), *Howard 15104, 15117* (A). PUERTO RICO: La Sardinera, *Britton 8508* (GH); Toa-alta, *Stahl 872* (GH).

This species is known as "babara" in Dominica and as the "black apple" in Montserrat. It is used as a fish poison in both areas.



ISOTYPE OF DIOSPYROS REVOLUTA POIRET. Specimen from the Botanical Museum, University of Copenhagen, collected by Ryan in Montserrat.

A NEW SPECIES OF PINUS FROM MEXICO[1]

JOHN W. ANDRESEN AND JOHN H. BEAMAN

THE SUMMIT of Cerro Potosí, possibly the highest mountain in the state of Nuevo León, Mexico, is encircled by a timberline made up of two species of pines. One of these is *Pinus hartwegii* Lindl., the dominant timberline species on the high volcanoes of southern Mexico. The other is a dwarf piñon not previously described. The pine which Muller (1937, 1939) called *P. flexilis* James is this species. The localities indicated by Martínez (1948, p. 108) under *P. flexilis* may refer to the new species, but the specimen he illustrated (p. 105, *fig. 72*) includes a cone which is definitely that of *P. flexilis*. We therefore cannot be certain that *P. flexilis* does not also occur on Cerro Potosí, although we did not find it there. The appearance of timberline on Cerro Potosí (FIG. 1) is similar to areas where *P. flexilis* occurs in the Rocky Mountains, but the two species resemble each other only in superficial habit and leaf characters. Their cones are very different. *Pinus flexilis* is a member of the subsection *Cembra*, group *Flexiles* (*sensu* Shaw, 1914). The new species belongs to subsection *Paracembra*, group *Cembroides*. Specimens in the Herbarium of the Chicago Natural History Museum were properly considered to belong to the piñon group by Dr. J. A. Steyermark, who, in 1940, annotated them as *P. cembroides* Zucc. The Schneider specimens in that Herbarium have also been previously determined as *P. quadrifolia* Parry ex Parl.

Pinus culminicola Andresen & Beaman, sp. nov. FIGS. 2–4.

DESCRIPTION OF THE SPECIES. Widely branching shrub 1–5 m. high with dense crown; leaves 5 per fascicle (rarely 4 or 6), 3–4.9 cm. long, 1–1.3 mm. thick, remotely serrulate, incurved in dense clusters at the ends of thick branchlets, glaucous ventrally, blue-green dorsally, stomata on ventral surfaces only, apices rounded and conspicuously cutinized; fascicle sheathes of young leaves 6–8 mm. long, stramineous, later becoming curled into persistent rosettes; conelets ovate, subsessile, single or in pairs, 8 mm. wide, 11 mm. long, rufous-brown, with short-mucronate scales; cones subglobose, 3.2–4.5 cm. long, 3.5–4 cm. wide; cone scales 50–60, inner and outer surfaces (exclusive of apophyses and seed cavities) stramineous; apophyses slightly raised, subrhomboidal, stramineous- to chestnut-brown, laterally keeled, convex above and below the umbo, those of the largest scales 1.8 cm. wide, 1.3 cm. high, 3 mm. thick; umbo dorsal, rhomboidal, minutely appendaged; seed-bearing cavity 9 mm. long, 6 mm. wide; seeds not seen, apparently unwinged, 1 or 2 per scale.

[1] Supported by grants G 9045 and G-15879 from the National Science Foundation and by a grant from the Scientific Council of the American Museum of Natural History.

DIAGNOSIS TYPICI EXEMPLARIS. Frutex, 1 m. altus, coma effusa; folia 3–4.9 cm. longa, 1–1.3 mm. crassa, quinque in fasciculo, ad margines remote serrulata, rigida, incurva densaque, ad terminos aggregata, ventrale glauca, dorsale caeruleo-viridia, cum stomatis solum ventralibus; vaginae 6–8 mm. longae, in brevi tempore crispae-rosulatae; strobilus subsessilis, subglobosus, 4.5 cm. longus, 4 cm. latus; squamae stramineae; apophyses subrhomboideae, fulvo-spadices, a latere carinatae, supra et subter convexae, maxima earum 1.8 cm. lata, 1.3 cm. alta, circa 3 mm. crassa; umbo dorsalis, rhomboideus, cum appendiculis minutis; cavum ubi semen positum 9 mm. longum, 6 mm. latum; semina ignota, evidenter sine alis, 1 vel 2 per squamam.[2]

FIG. 1. Aspect of timberline on Cerro Potosí. The dominant low shrub is *Pinus culminicola*. The erect, longer-leaved pine in the foreground and the tree on the horizon are *P. hartwegii*.

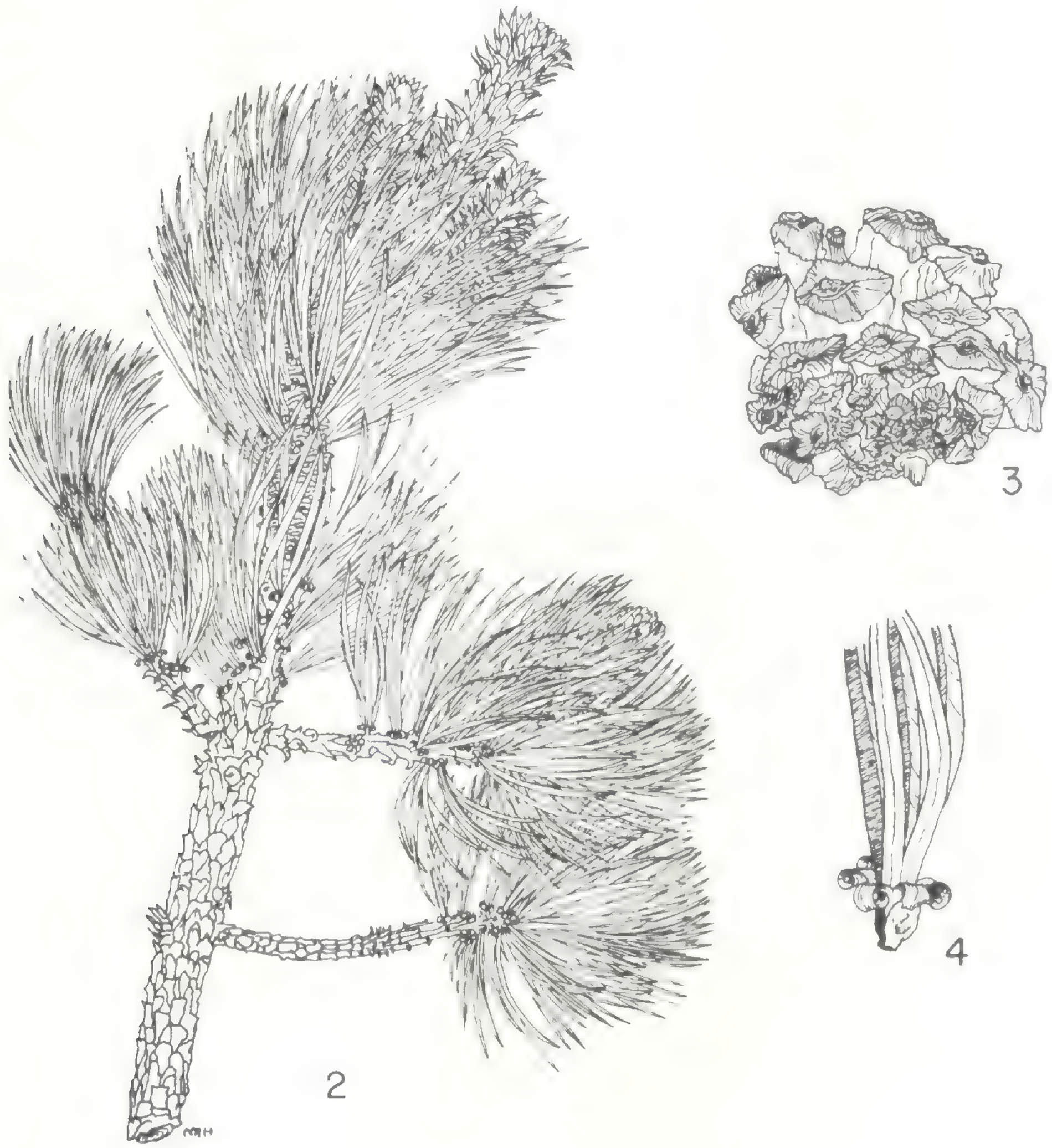
TYPE. **Mexico.** NUEVO LEÓN: Cerro Potosí, near top of mountain, ca. 3600 m. alt., in dense stand at timberline in soil weathered from hard, gray limestone, *Beaman 2675* (MSC 164008, holotype; A, US, isotypes).

OTHER SPECIMENS EXAMINED. NUEVO LEÓN: Northeast summit of Cerro Potosí, ca. 3650 m. alt., *Andresen 666* (MSC); Sierra Madre Oriental, ascent of Sierra Potosí by north hogback about 20 miles NE. of Galeana, alt. 11,600 ft.,

[2] We are grateful to Dr. Mladen Kabalin for editing the Latin diagnosis.

Mueller & Mueller 1241 (A, F, MICH, MO); the peak of Cerro Potosí, Municipio de Galeana, *Mueller 2261* (A, F, MICH, MO); at timberline on Cerro Potosí, Municipio de Galeana, 12,100 ft. alt., *Schneider 957* (F, 2 sheets).[3]

Only three species of piñons (*Pinus cembroides*, *P. nelsonii* Shaw, and *P. pinceana* Gord.) were recognized by Shaw (1914). *Pinus nelsonii* and *P. pinceana* are Mexican species with a limited distribution and conspicuous cone characters. *Pinus cembroides* (sensu Shaw) is widely distributed in the western United States and Mexico. Its variability is such that four



FIGS. 2–4. Branch, cone, and leaf fascicle of *Pinus culminicola*. *2*, Branch showing dense, clustered fascicles of incurved leaves and enlarging candle (× 2/3). 3, Cone with details of apophyses and umbos (× 2/3). 4, Portion of five-leaved fascicle with rosulate, persistent sheath (× 4 2/3). Drawings by Nancy R. Halliday.

[3] We appreciate the privilege of examining the specimens in the herbaria cited.

segregate species (*P. cembroides, sensu stricto; P. monophylla* Torr. & Frem.; *P. edulis* Engelm. in Wisliz.; and *P. quadrifolia*) have been maintained by several other authors. Shaw did not attribute much importance to the leaf characters by which these species can be distinguished, but to us they appear to have considerable value. The leaf differences are also correlated with cone characters of diagnostic value (cf. Little, 1950). Likewise, Mirov (1953) noted that the three species of the *P. cembroides* complex which he examined are not the same chemically. Differences between the species are evident in areas where their ranges overlap, suggesting the presence of genetic isolating barriers. The recognition of these taxa as species therefore seems preferable to the alternative of placing them at an infraspecific level.

Pinus culminicola and the four other species of the *P. cembroides* complex are separated from each other by characters of about the same magnitude. Probably the closest relationships of the new species are with *P. edulis* and *P. quadrifolia*. The most conspicuous character for distinguishing *P. culminicola* from its relatives is the five-leaved fascicle. Its cones are larger than those of *P. cembroides*, smaller than those of *P. monophylla*, and about the same size as those of *P. edulis* and *P. quadrifolia*. In habitat *P. culminicola* differs greatly from the other piñons which are found mostly in semiarid regions at the lower limit of forest vegetation. This species occurs in less arid circumstances at the upper forest limit. Probably no other species of piñon occurs as high as 3000 meters, while the lower altitudinal limit of *P. culminicola* is around 3400 meters.

Pinus culminicola and *P. cembroides* are essentially sympatric. The latter occurs abundantly near the base of Cerro Potosí (cf. Martínez, 1948, p. 85). We have compared the collection *Andresen 675* (MSC) of *P. cembroides* from 8 km. south of Galeana, Nuevo León, with *P. culminicola* and found the two species very different in characters of the cones, foliage, branches, and habit. The ranges of *P. culminicola* and *P. cembroides* are altitudinally separated but are close enough that pollen exchange is theoretically possible. Their distinctness is nevertheless maintained.

Since pines are conspicuous plants of considerable economic importance they have been frequently collected and studied. Probably almost all of the species of the genus are already known, but it is not entirely surprising that a new species should be found on Cerro Potosí where endemics are common. For example, Muller (1939) noted that six of 16 species he listed from the alpine meadow were collected for the first time in 1934 and 1935. The high elevation of the mountain (probably *ca.* 3650 meters), its geological age, and its wide geographical separation from the Rocky Mountains and the Mexican volcanoes are responsible for the high rate of endemism. As the flora of Cerro Potosí becomes better studied probably still more new species will be found there.

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FIBERS IN THE SECONDARY XYLEM OF AESCHYNOMENE

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WHILE WORKING on the petrified woods from the Deccan Intertrappean beds of India, I encountered a fossil wood which proved to belong to the genus *Aeschynomene*, of the family Leguminosae. In the course of this identification, doubts arose as to the proper interpretation of the ground-mass of the secondary xylem in *Aeschynomene*. Solereder (1908, pp. 275–276, *fig. 117a*; Taubert, 1894, p. 319) and Metcalfe and Chalk (1950, p. 523, *figs. 117a–d*) report that the parenchyma constitutes the greater part of the tissues in this genus and forms a ground-mass in which groups of fibers and vessels are distributed. Indeed, the elements of the ground-mass very much resemble those of fusiform parenchyma cells. However, my own investigation shows a different interpretation.

Thin sections of the woods of *Aeschynomene hispida* Willd. (Yw * 2169), *A.* cf. *aspera* L. (Yw 37202), A. *sensitiva* Sw. (Yw 43509), and an unidentified species (Yw 16552) were examined. These preparations were made from dried material in which, unfortunately the protoplasmic contents and the starch grains were no longer visible. Professor I. W. Bailey suggested that the ground-mass appeared to be composed of fibers. He further suggested that this could be confirmed from fresh material of *Aeschynomene* and by examining it without hydrofluoric acid treatment. Through the courtesy of Dr. P. T. Richards, of the Imperial College of Tropical Agriculture, Trinidad, West Indies, I secured fresh material of *Aeschynomene sensitiva* Sw. collected in Trinidad and preserved in formalin-acetic-alcohol. The present study is based on this material which was sectioned at 20–25 micra and stained in Haidenhain's iron-alum haematoxylin and safranin. A part of the wood was also macerated in chromic-nitric acid.

As the objective of this study was to ascertain the nature of the ground-mass of *Aeschynomene*, i.e., whether it is parenchymatous or fibrous, the observations given here are confined to the secondary wood. The microscopic examination of the cells forming the ground-mass shows that they are devoid of protoplasmic contents and do not possess starch grains (FIGS. 2, 5). This indicates their nonliving condition in the mature wood and, hence, their fibrous nature. It is interesting to note that this tissue shows a variety of cell structures, from libriform fibers to intermediate forms which are difficult to classify (FIG. 1b–f), culminating in a type of cell similar in shape to the fusiform cambial initials. In addition to these prosenchymatous cells, but excluding cells of ray parenchyma, there are other types in the secondary xylem which possess protoplasmic contents with nuclei, as well as starch grains (FIG. 6). These are the true

* Record Memorial Wood Collection, Yale University; citation of wood specimens as proposed by Stern and Chambers, Taxon 9: 1. 1960.

parenchymatous cells forming the longitudinal parenchyma of the wood. Their parenchymatous nature is also shown in some cases by the presence of septa, forming strands of two to four cells (FIG. 5). In the present species the longitudinal parenchyma is usually associated with the vessels in a scanty, abaxial and aliform to confluent distribution (FIGS. 2, 4).

A study of different forms of fiber and longitudinal parenchyma cells shows that the fusiform cambial initials differentiate two types of cells: (1) fusiform parenchyma cells, which may divide into parenchyma strands of two to four cells (FIGS. 5, 1b [1], b [2]), and (2) libriform fibers, with long, attenuated ends, which are associated with a series of cell types of various shapes, including those possessing a form like that of fusiform cambial initials (FIG. 1b–f).

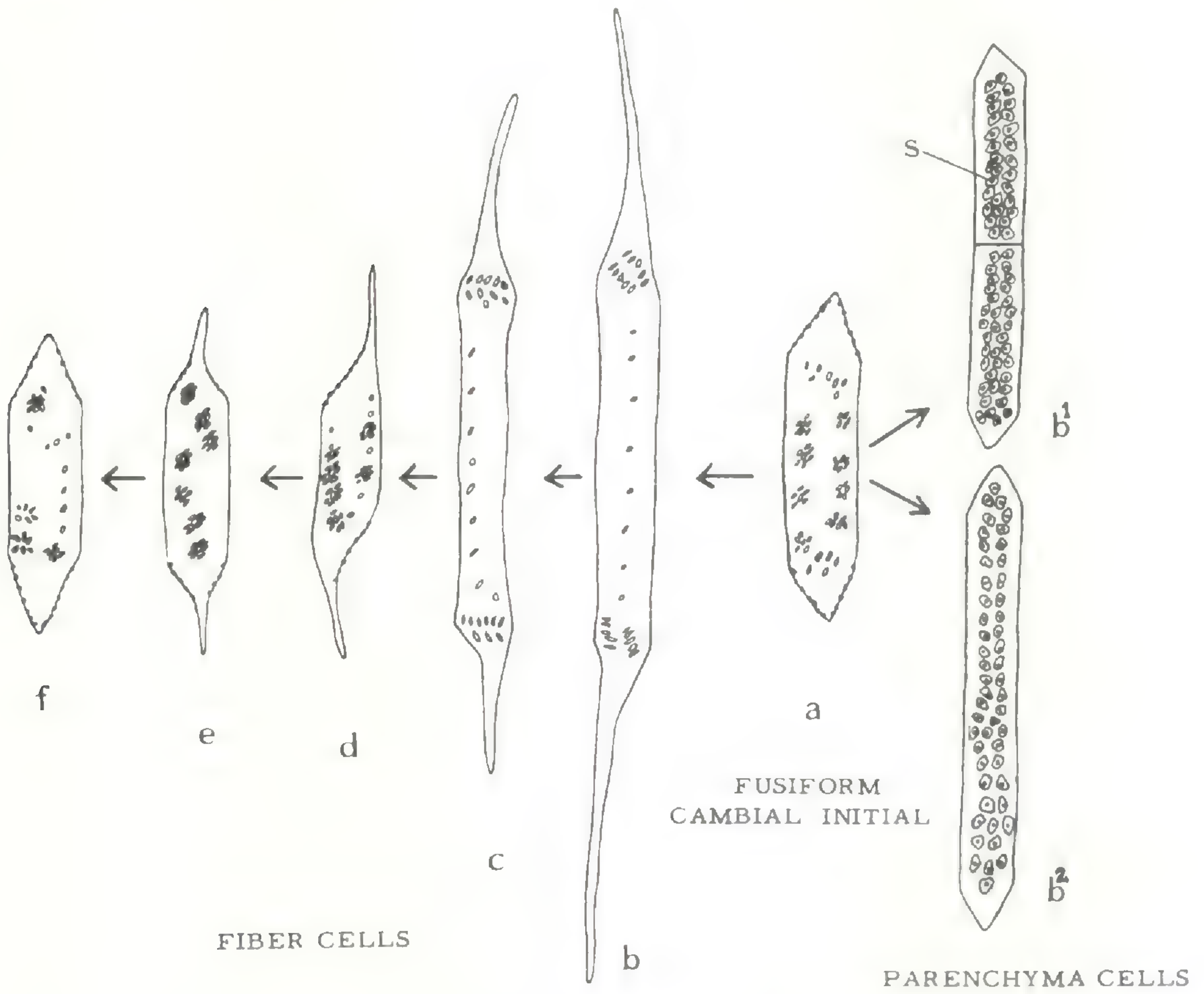

FIG. 1. Semidiagrammatic camera lucida sketch showing various types of fiber and parenchyma cells in *Aeschynomene sensitiva*, × 235. Parenchyma cells contain starch grains (s). See explanation in text.

From the above considerations it is quite evident that the fibers constitute the greater part of the tissues in the secondary wood of *Aeschynomene* and form a ground-mass in which the parenchyma and vessels are distributed. In view of these interpretations, the wood of *Aeschynomene sensitiva* Sw. is described below.

Growth rings: Not seen. *Vessels:* Small, 20–65 μ in tangential diameter

(mean 42 μ), chiefly solitary, occasionally in multiples of 2–4 cells or rarely in clusters (FIG. 2), quite uniform in size and evenly distributed, thin walled; solitary vessels mostly polygonal to oval in cross section. Vessel elements 90–210 μ long, with truncate to oblique end walls. Perforation plates exclusively simple, horizontal to slightly oblique. Intervascular pit-pairs vestured, alternate to opposite or subopposite, orbicular to oval in cross section, 7–10 μ in diameter, with linear to lenticular apertures, sometimes coalescent (FIG. 7). Tyloses absent.

Parenchyma: Paratracheal, scanty abaxial or vasicentric, sometimes forming irregular wings which rarely unite to form confluent parenchyma (FIGS. 2, 4); rarely isolated diffuse parenchyma cells also seen among the fibers. Parenchyma cells storied, thin walled, angular in cross section, 10–18 μ in diameter and containing nucleus, starch grains, cytoplasm, and protoplasmic contents (FIGS. 4–6). Parenchyma cells fusiform or in 2–4-celled strands (FIG. 5), sometimes chambered with solitary crystals in each chamber.

Xylem rays: Homogeneous (Kribs Homogeneous Type 3) composed of procumbent cells, storied, mostly uniseriate, sometimes biseriate (FIG. 5), rarely quite broad and containing vascular strands; uniseriate rays 1–24 (often 8–10) cells high; up to 10–15 rays per mm. Ray cells variously shaped, square, rectangular, oval to oblong and rarely pointed at one end, containing starch grains (FIG. 5).

Imperforate tracheary elements: Mostly thin walled, sometimes slightly thicker walled, especially near the vessels, and extending tangentially from them (FIG. 3), usually polygonal (mostly 5 or 6 sided) in cross section with large lumina, about 10–25 μ in diameter (FIGS. 2, 3, 4); nonseptate; storied (FIG. 5); pits simple, slightly more numerous on the radial than on the tangential walls, often appearing to be arranged in groups (FIG. 1b–f); pitting often markedly more abundant on and near the pyramidal walls. Cells variously shaped in longitudinal section (FIG. 1b–f), varying from libriform fibers to a fusiform type.

The author wishes to express his sincere appreciation to Professor Elso S. Barghoorn for his kind advice and for his critical reading of the manuscript. To Professor I. W. Bailey are extended many thanks for his help in cutting microtome sections of the wood of *Aeschynomene sensitiva* and for his many valuable suggestions. Dr. P. T. Richards, of the Imperial College of Tropical Agriculture, Trinidad, and Dr. William L. Stern (then curator of the S. J. Record Memorial Collection, Yale University), curator, Division of Woods, National Museum, Smithsonian Institution, Washington, D. C., have kindly made available woods of extant species of *Aeschynomene*, for which the author is greatly indebted. This study was completed while the author was a participant in the Visiting Research Scientists Program of the National Academy of Sciences, Washington, D. C., to which he is grateful for financial assistance.

DEPARTMENT OF BIOLOGY,
HARVARD UNIVERSITY

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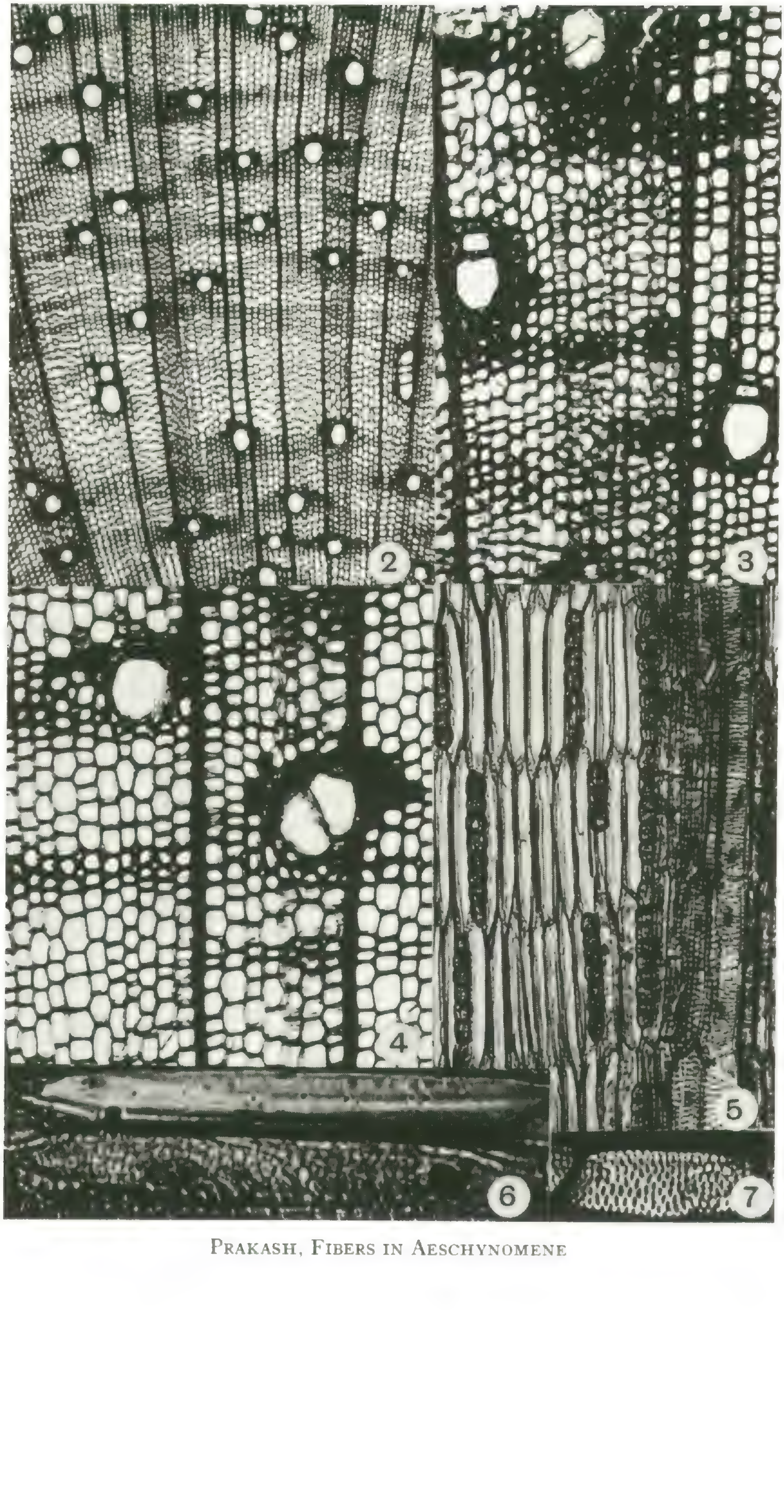
EXPLANATION OF PLATE

FIGS. 2–7. Modern wood of *Aeschynomene sensitiva*. 2, Transverse section, × 50 — note vessel and parenchyma distribution; parenchyma cells appear black due to presence of starch grains in them. 3, Transverse section magnified to show the distribution of thick-walled fibers × 140. 4, Transverse section magnified, × 140 — note paratracheal parenchyma with starch grains (shaded black). 5, Tangential section, × 140 — note storied rays, fibers, and parenchyma. 6, Longitudinal section of a parenchyma and a fiber cell, × 455 — note starch grains and nucleus in the parenchyma cell. 7, Intervascular pitting, × 180.



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THE DIRECTOR'S REPORT

The Arnold Arboretum During the Fiscal Year Ended June 30, 1961

The Staff:

It is with regret that we record here the death of Joseph Horace Faull, professor of forest pathology, *emeritus*. Professor Faull joined the staff of the Arnold Arboretum on July 1, 1928. A special laboratory was built for this area of research on the grounds of the Bussey Institution, and within a few years a greenhouse was added. Professor Faull, his students, and associates were among the first to recognize the significance of an arboretum with its massed collections of related species as a locale for the study of diseases of ornamental plants. To him and his team must go credit for the early work involving a service to the public in the identification and control of plant diseases now commonly carried on by state and federal experiment stations. From his laboratory came the early identification of a disease first found in this country in Ohio and now known as the Dutch elm disease. He warned prophetically of the danger of this fungus. In the course of his work, he and his students published studies of the fungal diseases of many genera of ornamental plants, including *Gleditsia*, *Cornus*, *Abies*, *Pinus*, *Picea*, and *Fagus*. Dr. Faull taught a class in forest pathology in Harvard College and guided the programs of nearly a dozen graduate students, many of whom have also achieved success in their field. Dr. Faull retired in 1940 but remained active in his laboratory for several additional years. Regrettably his position vacated during a shortage of skilled personnel concurrent with World War II could not be immediately filled and after the war was not continued due to a lack of funds. Dr. Faull's extensive herbarium of fungus diseases of cultivated plants was transferred to the Farlow Herbarium in Cambridge. Dr. Faull died on June 30, 1961, at the age of 91. A biographic report of his life will be prepared by his daughter, Dr. Anna Faull, for publication in a later issue of the *Journal of the Arnold Arboretum*.

On January 1, 1961, Mr. Peter S. Green joined the staff of the Arboretum. Formerly scientific officer at the Royal Botanic Garden, Edinburgh, Scotland, Mr. Green has been studying various genera of the Oleaceae, his special interest being in the cultivated genera *Osmanthus* and *Jasminum*. Mr. Green will continue his studies in this family, while at the same time serving as a horticultural taxonomist.

Dr. George K. Brizicky was appointed jointly with the Gray Herbarium to work with Dr. Wood on the flora of the Southeastern States. Dr. Brizicky replaces Dr. Kenneth A. Wilson, who resigned to accept a position at San Fernando Valley State College, Northridge, California.

Mr. Don M. A. Jayaweera, director of the Royal Botanic Garden, Peradeniya, Ceylon, and the holder of a Rockefeller Foundation Fellowship, was appointed as a Research Fellow at the Arboretum for the fiscal year. Mr. Jayaweera has worked with staff members in the herbarium on taxonomic problems of some cultivated and native plants of Ceylon and adjacent areas. He is also revising some of his work on the orchids of Ceylon through the use of the Orchid Herbarium of Oakes Ames, housed in the Harvard University Herbarium building.

Mr. Peter Tigerstedt, co-director of the Mustilla Arboretum, Mustilla, Finland, was appointed as the first Mercer Fellow at the Arnold Arboretum for the spring semester. Mr. Tigerstedt is the grandson of the founder of the Mustilla Arboretum who in the early days of the Arnold Arboretum was a correspondent of Charles Sargent. The Mustilla Arboretum, which is the northernmost in Europe, has received many plants from the Arnold Arboretum in past years. Mr. Tigerstedt took part in a variety of the activities of the Arboretum staff to acquaint himself with our methods and procedures.

The promotion of Dr. Lorin I. Nevling, Jr., to the position of associate curator of the herbarium was recommended and approved. Dr. Nevling also serves as assistant editor of the *Journal of the Arnold Arboretum*.

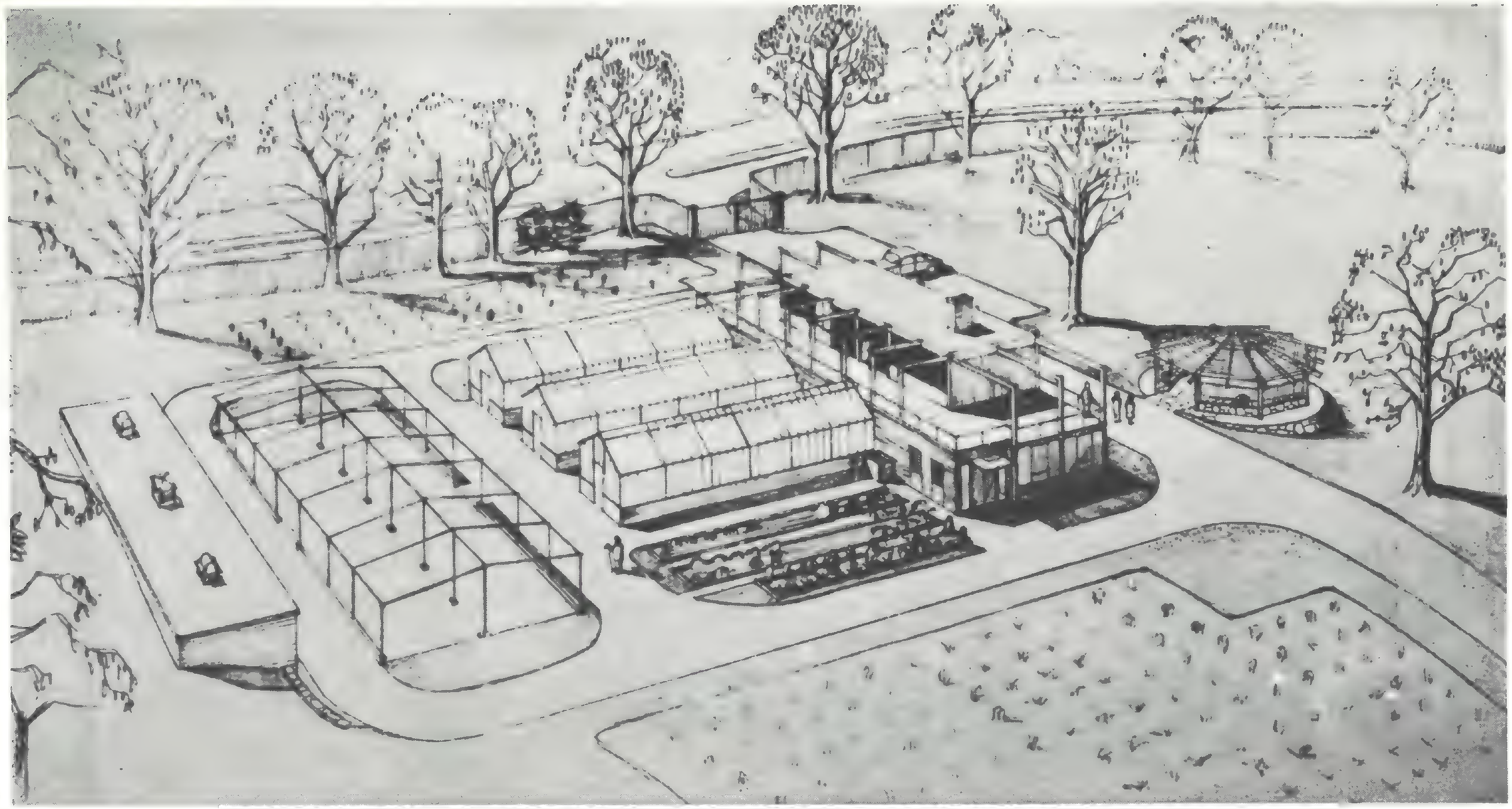
It is a special pleasure to record the honors awarded to several staff members. At the fiftieth anniversary of the College of Forestry, at Syracuse University, Irving W. Bailey, professor of plant anatomy, *emeritus*, was honored with the degree of Doctor of Science, *honoris causa*, with the following citation:

> IRVING WIDMER BAILEY, your name is synonymous with the role of research in the development of forestry. Your dedication to truth, zeal in research, and capacity to see the unexpected are gifts you have used to enhance and ennoble all the lives you have touched. Your solid and creative scholarship still guides and challenges forestry research. We honor you as forestry's preeminent wood anatomist and botanist and a truly inspired teacher."

Professor Karl Sax, professor of botany, *emeritus*, was honored on November 11, 1960, with a citation from the American Horticultural Council in annual meeting at Pasadena, California. Special notice was given to the many contributions in cytology and genetics and to the breeding of ornamental plants completed by Dr. Sax while an active staff member of the Arboretum.

Dr. Donald Wyman, horticulturist, was elected president of the American Horticultural Society for the coming year.

Two other resignations were accepted during the year. Miss Ann Close, business secretary, resigned and was replaced by Miss Anne Woolf. Miss Ann Waterman, assistant librarian, resigned to accept a position as librarian at the Pennsylvania Horticultural Society.



Architect's drawing of the proposed headhouse, greenhouse and associated construction to be built at 1050 Centre Street, Jamaica Plain, Massachusetts.

Horticulture:

Throughout the history of the Arnold Arboretum various directors have pointed out that in its location in the vicinity of Boston its plants are subjected to one of the most arduous and variable environments of any of the world's arboreta. Few areas of the world can show the vagaries of climatic conditions which our plants experienced during the past year. A summer of subnormal heat and rainfall was followed by the effects of hurricane "Donna" which hit the collections of the Arnold Arboretum on September 12, 1960. Although in comparison with hurricanes of previous years the loss was slight, our plants experienced severe branch damage which kept two tree pruners busy throughout the fall and winter months repairing and protecting the trees and shrubs affected by the strong winds. Although only thirteen trees were broken to a degree that required their removal, as frequently happens, three of these were trees familiar to the general public in conspicuous places on the grounds. The disfigurement of trees through the loss of branches, however, was severe. There are lasting effects of hurricanes in injury to root systems, and the growth of damaged specimens is generally poor in succeeding years. The superintendent and his staff succeeded in pulling to an erect position several dozen trees blown over by the storm.

Although we were fortunate in having a mild winter at first, allowing these plants to become re-established, our New England winter demonstrated once again the severity of environmental conditions in the area after the first of the new year. During February and March the Boston area experienced a record-tying cold spell when the temperature in Jamaica Plain did not rise above the freezing mark for twenty-six successive days. Subzero temperatures at night were frequent both during the period and in the days that followed. Fortunately, a heavy snowfall was on the ground during this period, and this, coupled with the heavy mulch which the staff deems desirable around the plants, protected the root systems. As a consequence this spring, irregular flowering or a complete lack of flowering in many plants that form flower buds in late summer and fall, the death of branch systems which necessitated heavy pruning, and the complete loss of many of the more tender species, were found. Throughout the "spring season" the Arboretum collections appeared to be behind what is considered the normal sequence of development. Much remains to be learned from continuing observation and recording of environmental conditions and subsequent flowering of plants in the Arboretum collections. The development of new greenhouse facilities for the Arboretum should allow not only the experimental duplication of some of these unusual environmental effects but a complete testing of the variations in the handling of such plants as an aid to their survival in our area.

The approval in principle by the President and Fellows of Harvard University as trustees of the Arnold Arboretum for the construction of a headhouse and new greenhouses for the Arboretum was reported last

year. During the current fiscal year much time and effort have been spent on this development, and it is a pleasure to report that construction is now under way. The firm of Griswold, Boyden, Wylde and Ames, of Boston, was selected as the architects and approved by the Corporation. The plans developed were discussed and checked with the staff members involved in each field, for the new greenhouse will house the propagation staff, a laboratory suitable for morphological, cytological, and genetical investigations, and a conference room for staff meetings and discussions. The main building (the headhouse) is designed to facilitate work in the area of propagation of woody plants, equipped as it will be with cold chambers for experimentation for hardiness, seed dormancy, flower initiation, and general problems of plant growth as these are related to the Arboretum's interests. A small apartment will be located on a second floor to enable a staff member to live on the grounds and be associated with the continual care which nursery and greenhouse collections require. Three greenhouses (with space for a fourth) are provided with automatic controls, insofar as possible, offering several environmental areas for experimentation. A pit house with a mechanism for heating and cooling is capable of extending either a warm fall or a cold spring season and will offer numerous research possibilities. A hexagonal display house for *bonsai* and a shade house for nursery stock complete the construction plans. The entire area will be surrounded by a chain link fence which hopefully will afford a security lacking in our present nursery area.

The new location, to be known as 1050 Centre Street, represents land acquired as three purchases in 1924, 1926, and 1927 from the Adams Nervine Hospital. Purchase at that time was by means of special contributions for the purpose. Regrettably, all of the top soil had been removed from one area prior to its sale, and in recent years this land has been of little value. Currently a program is under way to replace the top soil and to build up the fertility of the area for its future use for nursery or display plants. Fortunately, an abundance of top soil, which can be used for regrading the greenhouse area, has been encountered in the excavations for the basement of the headhouse and for the pit house. A new road will be constructed from the Arboretum proper, departing from the existing road system near the upper part of the lilac collection. This entrance will reduce the need to enter or depart from the busy Centre Street section.

The new greenhouses will allow a further development of many aspects of the work of the Arboretum staff. The greenhouses will not contain display collections and will not normally be open for public inspection but will function in the scope of the indenture which established the Arnold Arboretum for the growth and study of plants hardy to New England and for the research of the staff. The construction of the greenhouses at this time without a special financial drive for construction funds is possible by the use of the income from the bequest of Mrs. William Dana Mercer. A suitable plaque is planned for the interior of the building. A ground-breaking ceremony was held on May 12th during

a meeting of the Board of Overseers' Committee to Visit the Arnold Arboretum. Token shovels of soil were lifted by Dr. Bradford Washburn, chairman of the committee; Dr. Nathan M. Pusey, president of Harvard University; Dr. George M. Taylor, director of the Royal Botanic Gardens, Kew, both as a member of the Visiting Committee and in behalf of other arboreta; Mr. Martin Walsh, chairman of the Board of Park Commissioners of the City of Boston; and by Dr. Howard, director, for the Arboretum staff. Construction and occupancy are expected to be completed during the next fiscal year.

Breaking ground for the new greenhouses of the Arnold Arboretum, May 12, 1961. Front, left to right: President Nathan M. Pusey, Mr. Martin F. Walsh, Dr. Bradford Washburn, Dr. George Taylor, and Dr. Richard Howard. Rear, left to right: Mr. Lincoln Boyden, Jr. (architect), Dr. Donald Wyman, Mr. D. M. A. Jayaweera, Mr. Chester E. Bond (contractor), and members of the Committee to Visit the Arnold Arboretum, including far right, Mr. Sidney Shurcliff.

In a continuation of the annual maintenance program for the Arboretum grounds the Department of Parks and Recreation of the City of Boston rebuilt or replaced all of the concrete and wood-slatted benches in the Arboretum. These reconditioned benches freshly painted a dark green make the grounds more attractive for the visitors. The department was also responsible for painting the gates to the Arboretum and for the replacement of defective fire hydrants within the grounds.

It is hoped in future years to continue to resurface many of the roads within the Arboretum and to complete the fencing of the property. Regrettably the Arboretum has never been completely fenced, and theft

and vandalism continue. In spite of increased protection supplied by the Boston Police Department twenty-five choice evergreens were stolen during the year, some within twenty-four hours of being planted. Miscellaneous acts of vandalism continue and are annoying and expensive in the demands on staff time. Various steps for better protection are under consideration. Currently the roadway gates at the Arboretum are open from sunrise to sunset and the pedestrian gates continuously, although the staff is present only during the usual working hours. A staff police force or a restriction in the visiting hours may be required within the next few years, but a sizeable expenditure for fencing must be made first.

During the year about 280 species and cultivars were added to the Jamaica Plain collection from the nursery area in Weston. Included were approximately 60 *Rhododendron* plants which were added to the steep bank-planting on Hemlock Hill near the South Street gate. Additional selected lilac plants were placed near the walk in the lilac collection to continue a program of revising this collection to display all of the cultivars considered in the Lilac Committee's list of 100 best varieties. Additional plantings were made on the outcrop of Roxbury conglomerate known as the "rockery." It is hoped that dwarf plants and a heavier mulch will aid plants to survive in this difficult yet intriguing area. We were fortunate to continue to receive horse manure for the trucking and have added each week about six truck loads obtained from local stables. Smaller amounts of wood shavings, approximately one truck load per week, are donated for the hauling by a local lumber yard, and a truck load of cocoa shells was donated by the Hershey Chocolate Company with delivery supplied.

The hedge collection located near the Bussey Building has received special attention during the year. It is planned to relocate this collection near the new greenhouses. Ground has been prepared for these plants and the old collection has been root pruned in preparation for moving.

In October 1960, the Arboretum staff was notified that legislation filed by Representative James J. Craven, Jr., of Ward 19, had been approved by the General Court. This act provided for a swap of land involving a 17-acre tract of property owned by Harvard but adjacent to Arboretum property, between South Street and the New Haven Railroad for land owned by the Metropolitan District Commission in Randolph, Massachusetts, and a cash settlement. The Randolph property would then be used by the Medical School with another cash settlement to the Arnold Arboretum. There was considerable publicity during the election campaign of the benefits to the public of the playground and picnic area planned adjacent to the Arboretum. Although this transfer of land title may occur eventually, legal considerations have delayed positive action. All of the *Salix* and *Populus* species which grow in the marshy tract have been propagated for replanting elsewhere on the grounds.

Many of the activities of the propagator and his assistants were concerned with the design and the future relocation of the greenhouse. Thus,

ABOVE: A portion of the collections of *Rhododendron* and *Cytisus* species on Bussey Hill.

BELOW: Placing a barrier to protect small plants against sledding.

during the year 363 taxa in our general collections were propagated, these representing plants too large to be moved, plants needing replacement due to age or condition, or plants represented by insufficient individuals in our general plantings. In addition, another 103 taxa were propagated

from our general collections in response to specific requests from other gardens or individual scientists. The Arboretum staff members made requests for propagating material of 116 taxa for use in experimental or taxonomic or cytological studies. The propagator has also collaborated with the taxonomists in supplying information on propagation to be published with taxonomic studies of cultivated plants. For experimental projects involving the hardiness of cuttings or young plants 76 taxa were processed, and 104 taxa as seeds and 49 taxa as cuttings were subjected to experimental procedures for information relative to improving techniques of propagation of these taxa. During the fiscal year a total of 270 shipments of plant material comprising 1105 taxa was sent to co-operating nurseries and other arboreta in the United States and twelve other countries. Of these, 190 were sent as seeds and 915 as cuttings or plants, indicating the growing need and desire for reliable propagating material to represent the taxon and the lessening interest in seeds with their possibilities for hybrid contamination. From other sources representing the United States and 21 other countries, the Arboretum received 227 shipments of living plants or propagating materials comprising 705 taxa and 47 shipments of seeds of 118 taxa.

Experimental work conducted in the greenhouses concerned the germination of various kinds of seeds, the rooting of cuttings or plants usually propagated by grafting or considered difficult to root, and additional work on the length of storage time that cuttings of different taxa may be held under different conditions. In co-operation with the work of Mrs. Claude Weber on *Chaenomeles*, Mr. Fordham determined that a stratification of two months at 41°F. was the best method for producing a uniform stand of seedlings most quickly. Seeds of the fringe tree (*Chionanthus retusus*) responded most satisfactorily to three months of warm stratification, followed by three months of cold stratification at 41°F. A similar treatment applied to seeds of *Hamamelis mollis* proved equally successful to the five month warm period usually recommended.

Special attention has been given to several members of the Hamamelidaceae. Experimental work with the rooting of cuttings of *Parrotia* showed that grafting these plants as most nurseries do traditionally is not necessary. Cuttings taken from a 79-year-old specimen of *Parrotia persica* in the Arboretum collection on June 23, treated with Hormodin No. 2 or No. 3, and maintained with bottom heat of 73°F. under plastic had rooted 100% by September 10. A control lot without hormone rooted only 14%. Rooting at this time was heavy and the plants could have been removed and potted earlier. The potted plants produced additional growth before going dormant, and all survived the winter, an unusual condition for *Parrotia* which has a reputation for poor survival of rooted cuttings.

The house at 383 South Street formerly occupied by Professor Johnston was renovated, including modernization of the plumbing, painting of the exterior, and roofing, as a portion of our program of building maintenance.

Case Estates:

During the year an increase in the number of visitors to the Case Estates in Weston has become evident. The annual "open house" held in early May was well publicized to the "Friends of the Arboretum" and in the papers of adjacent communities. The attendance was gratifying to the staff members on duty there to answer questions. Many of the visitors have made repeated visits for subsequent study. The ground cover plots and the perennial garden vie for principal interest. The Case Estates remain primarily a nursery area for the Arboretum, however. To increase the beauty of the grounds, surplus plants have been placed where they will be seen better by the visitors or those driving by. The spectacular flowering of *Malus* 'Henrietta Crosby' this year created traffic tie-ups on Wellesley Street as drivers slowed to admire this handsome row of ornamental apples. We anticipate that the developing plantings near the High School and along Ash Street will soon draw comparable interest.

This spring saw the first flowering of the test plots of *Narcissus* taxa planted by Dr. Helen Scorgie and other members of the New England section of the American Daffodil Society. Approximately a hundred varieties were in flower during the "open house," and Dr. Scorgie was kind enough to answer the many questions posed by the admirers of these plants.

An exhibit of Christmas decorations and the plant materials used in making them. Staged at Horticultural Hall, Boston, Massachusetts, November 28–December 2, 1960.

It was from the nursery areas that plants were sent to the "co-operating nurserymen" during the year. Young plants of *Buxus sempervirens* 'Vardar Valley,' *Cornus pumila*, *Euonymus europaeus* 'Red Cascade,' *Rhododendron* 'Mandarin Red,' *Sorbus cashmiriana*, and *Viburnum plicatum* 'Lanarth' were made available to 90 nurseries and arboreta which requested plants from a circulated list. Other surplus plants were again made available to the Department of Buildings and Grounds of Harvard University for plantings around university buildings in Cambridge. A large general collection was also given to Union College, Schenectady, New York, to increase the small arboretum maintained on that campus.

It has been pointed out previously that the Case Estates in Weston experience more severe cold than does the Arboretum proper in Jamaica Plain. During the past winter, specimens of *Deutzia* showed comparable die-back in each area due to the cold, but many clones of *Rhododendron fortunei* suffered more in Weston than did comparable plants in Jamaica Plain.

The wildlife of the area is again on the increase and the destructive effects of rabbits and woodchucks were evident after the winter snow disappeared. Deer have been seen on the property on two occasions; pheasants are numerous; and a covey of quail appeared again for the first time in several years.

Land was again made available to staff members of the Bussey Institution and the Cabot Foundation of Harvard for growing experimental plants in Weston.

Education:

Only one formal course was offered during the spring semester when Dr. Howard taught a class in horticultural taxonomy in Harvard College. Dr. Thomas offered special work in cytotaxonomy to a group of graduate students working both in Cambridge and with the living collections in Jamaica Plain. The staff participated in the regular series of weekly seminars on taxonomic subjects.

Four classes were offered to the general public at Jamaica Plain or Weston in the fall, two field classes in the spring, and a class in propagation which met at appropriate intervals during the year. During the spring semester a lecture series was offered evenings in the Administration Building and was well attended. These lectures, designed to be semitechnical in nature, were presented by various staff members and research fellows.

The usual service of guided tours of the Arboretum plantings both in Jamaica Plain and Weston was accepted by many garden clubs, women's clubs, and civic groups during the fall and spring seasons. The spring tour offered jointly by the Massachusetts Horticultural Society and the Arboretum drew a large crowd which was accommodated in eight busses. A staff member in each bus led the groups through some of the more floriferous areas of the Arboretum while explaining the plants and

answering questions. These trips seem to be particularly worth while, for a large percentage of the people return for more leisurely walks alone or with smaller groups.

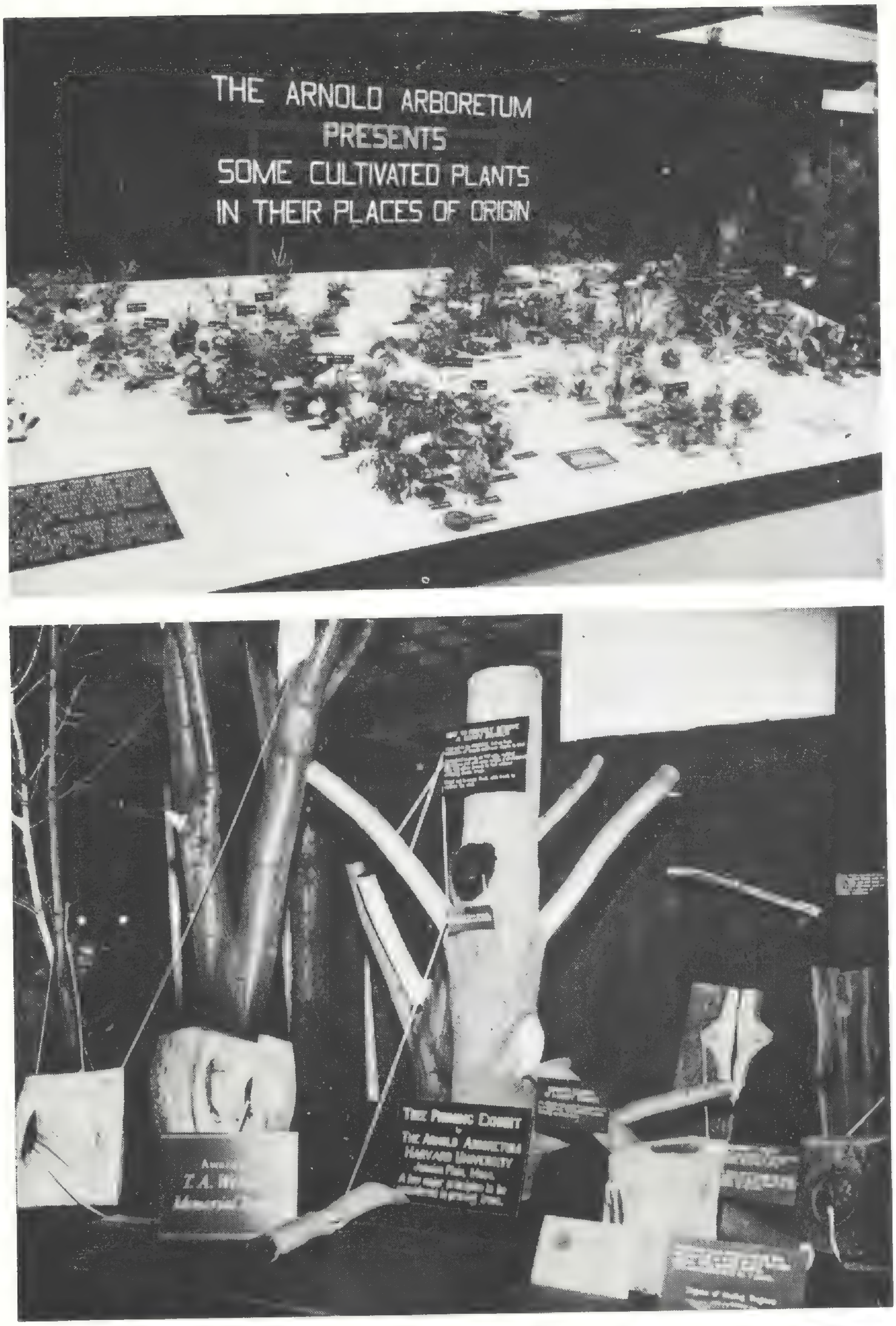
Arboretum staff members spoke to many garden clubs, horticultural groups, and similar organizations during the year. In addition, a set of kodachrome slides of the plants and activities at the Arboretum with a printed commentary was made available to other groups for their own programming. Dr. Wyman was the principal speaker at the thirtieth anniversary luncheon of the Holden Arboretum in Cleveland, Ohio. Dr. Wagenknecht described registration procedures at the organizational meeting of the American Boxwood Society in Boyce, Virginia, and at the annual meeting of the New England section of the American Society of Horticultural Science. Mr. Fordham presented a paper on double-dormant seeds at the Plant Propagators' annual meeting at Cleveland. Dr. Wood presented a series of lectures in a program in plant evolution in the Department of Biology at Vanderbilt University, Nashville, Tennessee. Drs. Perry and Hu presented papers at the annual meeting of the Society for Economic Botany held in Boston. Dr. Howard spoke on the campuses of Union College, in Schenectady, New York, and Mount Mercy College, in Pittsburgh, Pennsylvania, under the sponsorship of the American Institute of Biological Sciences. He also opened the lecture series at Longwood Gardens, was a speaker at the annual meeting of the New England Nurseryman's Association, and presented the commencement address at the graduation exercises at the State College, Bridgewater, Massachusetts.

Exhibits and Displays:

Five flower-show exhibits were prepared by the Arboretum staff during the winter and spring. A display of Christmas decorations and the plants comprising them, formerly held in the Administration Building in Jamaica Plain, was staged at Horticultural Hall, Boston, in co-operation with the Massachusetts Horticultural Society. When held previously at Jamaica Plain the show had had only a moderate attendance due to our more isolated location and the inadequate local transportation. Horticultural Hall proved to be an excellent location, however, and the exhibit was well attended. Members of several garden clubs under the leadership of Mrs. Donald Wyman prepared swags, wreaths, decorations, and arrangements, while the Arboretum staff prepared specimens and descriptive data of the plant materials involved.

The Arboretum exhibit at the Massachusetts Horticultural Society's Spring Flower Show showed numerous cultivated plants in their area of origin. A Mercator projection map of the world, 40 feet by 10 feet allowed small plants to be placed in that section of the world where each plant was native. One hundred and seventy-eight plants could be accommodated in this educational exhibit. It was awarded a first prize and a gold medal.

The Arboretum's tree pruning exhibit was set up at the International Flower Show of the New York Horticultural Society held in the Colli-



ABOVE: The Arnold Arboretum exhibit at the Spring Flower show of the Massachusetts Horticultural Society, Boston, Massachusetts, March 11–19, 1961.

BELOW: The Arnold Arboretum exhibit at the International Flower Show, New York City, March 4–12, 1961.

seum. Mr. Robert Williams, superintendent of buildings and grounds, receives full credit for this informative exhibit which won a first prize, a gold medal, and the T. A. Weston trophy for the most educational exhibit in the show.

The Arnold Arboretum *bonsai* collection was displayed in Detroit, Michigan, for the flower show of the Michigan Horticultural Society. The dwarf plants displayed in an oriental setting won a gold rosette, the highest award of the show.

Finally, in late spring, the New World portion of the exhibit used for the Massachusetts Horticultural Society show was reconstituted using later flowering materials and was exhibited by request at the flower show sponsored by the Federated Garden Clubs of Massachusetts at the Jordan Marsh Company, Boston.

Comparative Morphology:

Professor I. W. Bailey served again this year as curator of the wood collection. His continuing care and interest are greatly appreciated. During the year a sizeable number of wood samples were made available to the Quartermaster Research and Engineering Command, U.S. Army, for a specific chemical analysis of cellulase inhibitors, a program of research conducted at their headquarters in Natick, Massachusetts. In addition, requests for wood samples of various genera and families were received from fourteen individuals and institutions and all were filled as completely as possible.

The research program of Professor Bailey, supported in part by a grant from the National Science Foundation, continues to concern the putatively primitive leaf-bearing genera of the Cactaceae. Papers summarizing his research will continue to appear in the *Journal of the Arnold Arboretum*.

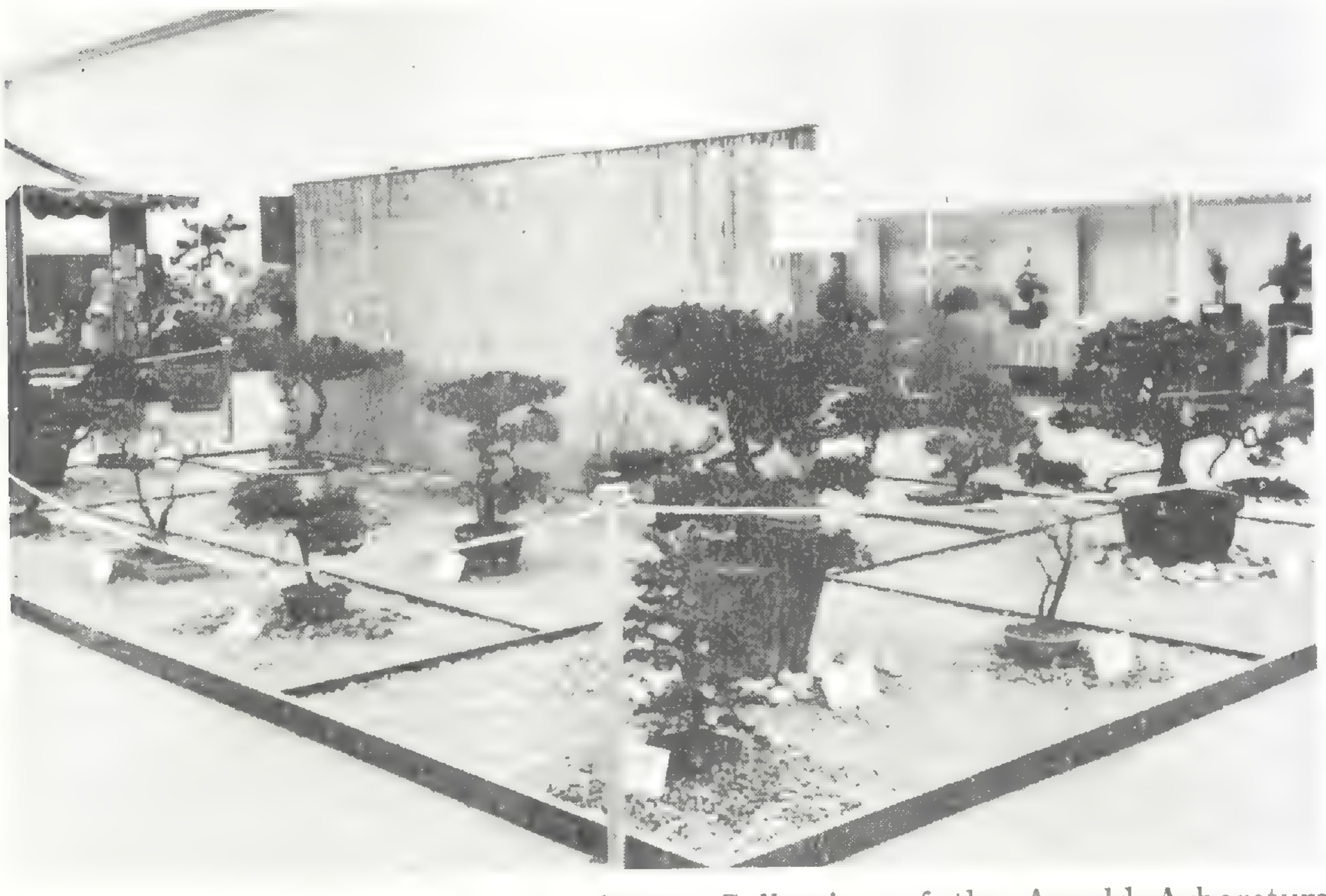
Dr. Uttam Prakash, of the Birbal Sahni Institute of Palaeobotany, Lucknow, India, has been a visiting scholar for a second year and has continued to use the wood and slide collections of the Arboretum in connection with his investigations of fossil floras of the state of Washington.

Library:

The attention of the librarians was devoted in considerable extent to a reorganization of the horticultural section of the library located in Jamaica Plain. The books formerly shelved on the second floor of the herbarium were moved to the third floor and rearranged on the shelves in the main reading room and in the alcoves, thereby freeing the second floor space for an increase in the herbarium of cultivated plants.

Three hundred and twenty-three volumes were added to the library, increasing the total to 51,106 on June 30, 1961. Nine hundred and seventy-two pamphlets were added to the monographic collection, making a total of 18,302. A total of 2,182 catalogue cards was added to the main file. Two hundred and seven books were bound or rebound, and fifty old

books given special restoration service. Miscellaneous indices also received their regular accessions. Three thousand cards were added to the Gray Herbarium Card Index of American Plants, 4,000 cards to the Torrey Index of American Botanical Literature, and approximately 700 cards to the Rehder index of cultivated plants. Sets 12–14 of the Index Nominum Genericorum were also filed.



Japanese *bonsai* of the Lars Anderson Collection of the Arnold Arboretum on exhibition at the Flower Show of the Michigan Horticultural Society, Detroit, Michigan, February 25–March 5, 1961.

Although "Xerox" reproduction service became available through the Widener Library and was recommended whenever possible, 120 books nevertheless were sent out on Interlibrary loan. Twenty-five books were borrowed from other libraries.

Herbarium:

During the year 12,208 specimens were mounted and added to the herbarium, bringing the total collection to 726,344 specimens on June 30, 1961. During the same period 17,232 specimens were received through exchange, gift, subsidy, or for identification. This year the largest number represented a subsidized collection made by Dr. Hugh M. Raup in the Mackenzie Basin of Canada in 1938. A sizeable collection of native and cultivated plants of Japan was purchased from Mr. Miyoshi Furuse. A total of 3,345 specimens was distributed to other institutions in exchange.

The staff filled 113 requests for herbarium specimens on loan, representing 14,614 specimens sent to 65 institutions, forty-three of these in the United States. The staff requested 65 loans totaling 3,399 specimens

for study from 38 institutions, including twelve in the United States. The incoming loans averaged 52 specimens, while the outgoing loans averaged 129 specimens.

The additions to the herbarium of cultivated plants housed in Jamaica Plain have now reached the point where many of the cases are crowded. Fortunately, space for expansion is available, and new steel herbarium cases have been ordered. A general shift of this herbarium is being planned. Much of the material added to the cultivated herbarium represents cultivated herbaceous plants or exotic greenhouse plants. We appreciate very much a large exchange of specimens from the comprehensive collections of the Longwood Gardens, nearly all of which represent new genera or species for our herbarium. This material will assist materially in the routine identifications of many of the specimens sent to us for naming.

The publications of the taxonomists cited in the bibliography of the staff clearly indicate the diversity of area and plant groups represented in their research.

Travel and exploration:

The Arboretum was represented at various annual science meetings in several parts of the country by staff members. These meetings included those of the American Association of Botanical Gardens and Arboretums, the American Institute of Biological Sciences, the American Horticultural Council and American Horticultural Society, the Plant Propagators Society, the Society for Economic Botany, the National Shade Tree Conference and the American Society of Horticultural Science.

Field work was undertaken by Dr. Howard, in Montserrat, St. Croix, and Redonda; by Dr. Wood, in central Florida with Dr. George R. Cooley; by Dr. Wagenknecht, in Virginia and North Carolina; and by Dr. Thomas, in Florida and Alabama. In all cases, herbarium specimens and living plant materials were brought back for addition to the Arboretum collections.

Dr. Kobuski spent two months in Europe visiting herbaria in Scotland, England, Switzerland, and Sweden in connection with his principal research interest in the Theaceae and was engaged especially in the examination of types and other herbarium materials of the Old World species of *Ternstroemia* which he is revising.

The Arboretum has also contributed to the support of several collectors working in Japan; to an expedition of Mr. James Keenan, of the Royal Botanic Garden, Edinburgh, to Burma; and to the work of Mr. Theodore Dudley, in Turkey. These areas may yield plants of horticultural value to the Arboretum and specimens for the herbarium.

Gifts and grants:

The annual appeal to the Friends of the Arnold Arboretum received its usual generous response. To all of these contributors we extend the

appreciation of the staff for the support which makes possible extra services to the area of horticulture. A special gift from Dr. George R. Cooley supports the work of Dr. Wood and his collaborators on the generic flora of the southeastern states.

During the year we have received an unusually large number of books, pamphlets, and research materials for the library from the estate of Dr. Franklin P. Metcalfe, and from Mrs. Susan D. McKelvey, Mr. P. Bernat, Dr. H. Field, and Dr. A. F. Hill. These contributions materially increase the value of our library and pamphlet collections.

Plant materials have been received in exchange from many sources, but the gift of living plants for the education classes received from Mr. Robert Pirie, of Hamilton, Massachusetts, is particularly appreciated. I also wish to acknowledge the assistance of the many individuals who have supplied propagating material, photographs and information in response to specific requests for research projects of the staff. The largest number of requests concerned the monograph of *Chaenomeles* being prepared by Mrs. Claude Weber.

Publications:

The regular publications of the Arnold Arboretum include the quarterly *Journal of the Arnold Arboretum* and *Arnoldia*, which is issued at irregular intervals. Both appeared as planned. A double number of *Arnoldia* issued during December, 1960, comprised a revision by Dr. Wyman of his earlier publication, "How to Establish an Arboretum or Botanical Garden." The first edition of this article is out of print, and the demand for reprints of the revised edition exceeded all expectations.

Five numbers of *Arnoldia* dealt with the registration lists of cultivar names and the problems of preparing such lists. The council of the American Association of Botanical Gardens and Arboretums requested 175 extra copies of each list for distribution to its membership, and many additional requests for reprints from nurserymen indicate the interest in these bibliographic listings. To the present, registration lists for cultivar names in *Cornus*, *Gleditsia*, *Forsythia*, *Liquidambar*, and *Pieris* have been published.

The librarian was also responsible for the photoprint reproduction and the distribution of Shaw's *Pines of Mexico*. Published originally by the Arboretum in a limited edition, this work has long been out of print. To date, the sales of the photoprint reproduction have exceeded the distribution of the original printing.

This report would not be complete without acknowledging the efforts of Miss Ethel Upham, of East Woodstock, Connecticut, who for many years has painstakingly prepared the index for the *Journal of the Arnold Arboretum*. Miss Upham has now relinquished this arduous but invaluable task which passes from her capable hands to others.

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1960–1961

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